SEX DIFFERENCES IN PARENTAL ROLES AND DIVING BEHAVIOUR OF THICK-BILLED MURRES, URIA LOMVIA, AND RAZORBILLS, ALCA TORDA, AT THE GANNET ISLANDS, LABRADOR

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SEX DIFFERENCES IN PARENTAL ROLES AND DIVING BEHAVIOUR OF THICK-BILLED MURRES, *URIA LOMVIA*, AND RAZORBILLS, ALCA TORDA, AT THE GANNET ISLANDS, LABRADOR.

By

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Para mi loquisimo amor Steve

y mis adorados

Andrés y Sebastian

ABSTRACT

There is no evolutionary, ecological or behavioural explanation for the partitioning of parental roles between the sexes in the Alcini, which includes murres (*Uria*), the razorbill, (*Alca torda)*, great auk (*Penguinus impennis)* and dovekie (*Alle alle)*; and why the male is the selected sex to accompany the chick to sea. I investigated parental roles and diving behaviour of two sympatric alcids, thick-billed murres, *Uria lomvia*, and razorbills, at the Gannet Islands, Labrador to determine whether sex-specific differences in energy expenditure at the time of departure explain male-only care at sea. Externally attached time-depth recorders (TDRs) negatively affected parental behaviour in male and female thick-billed murres. Partners of TDR-equipped birds compensated for the reduced parental effort in brooding and chick provisioning of their mates, with no differential responses between sexes. There was a temporal segregation of water depths, dive profiles, and food resources between the sexes in both species; these differences being stronger in thick-billed murres than in razorbills. Most murre females' self-feeding diving coincided with the vertical migration of crustaceans to surface waters; while male's self-feeding foraging occurred when prey were in deeper sections of the water column. Chick-provisioning diving was deeper than self-feeding irrespective of the sex or the time of day, suggesting equal parental effort allocation of the sexes underwater. Nevertheless, males had longer foraging trips than females probably due to the time spend flying to farther locations than females. Higher self-feeding rates and closer feeding locations may

explain female's higher delivery rates at the breeding site. The longer time males spent brooding the chicks may serve to ensure parent-offspring vocal recognition at departure. Larger bill dimensions and higher levels of aggressive behaviour may confer males a better ability to protect the chick. In conclusion, differences in energy expenditure between the sexes did not seem to explain the male's parental role at sea. Instead, I proposed that the patterns of parental roles found between sexes was the result of a chain of events favouring male involvement in chick brooding and care at sea. A higher level of aggressiveness of the parent that escorts the chick to sea may have been selected for to ensure offspring survival, and as a result, parental roles developed at the breeding site to ensure male-only care at sea.

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CHAPTER 1: INTRODUCTION

1.1 STUDY SPECIES

Seabirds' life history charactheristics differ notably from those of land birds; in general they live longer and produce fewer offspring that require extensive parental care until they mature (e.g. Schreiber & Burger 2001). As a result, both sexes provide parental care (biparental care) and retaim the same mates for several seasons or lifetime (social monogamy; e.g. Brooke 2004) to increase survival and lifetime reproductive success (fitness). Some seabirds, such as auks (or alcids) and petrels, spent considerably more time at sea and use land mostly for reproduction (marine birds). Alcids are highly specialized and ecologically diverse group of marine, wing-propelled pursuit-diving birds (Nettleship 1996). Phylogenetically, the family Alcidae is located in one of two major groups in the order Charadriformes along with the clade of gulls, terns, skimmers and jaegers (Sibley and Ahlquist 1990; Ericson *et al.*2003; Fig. 1.1).

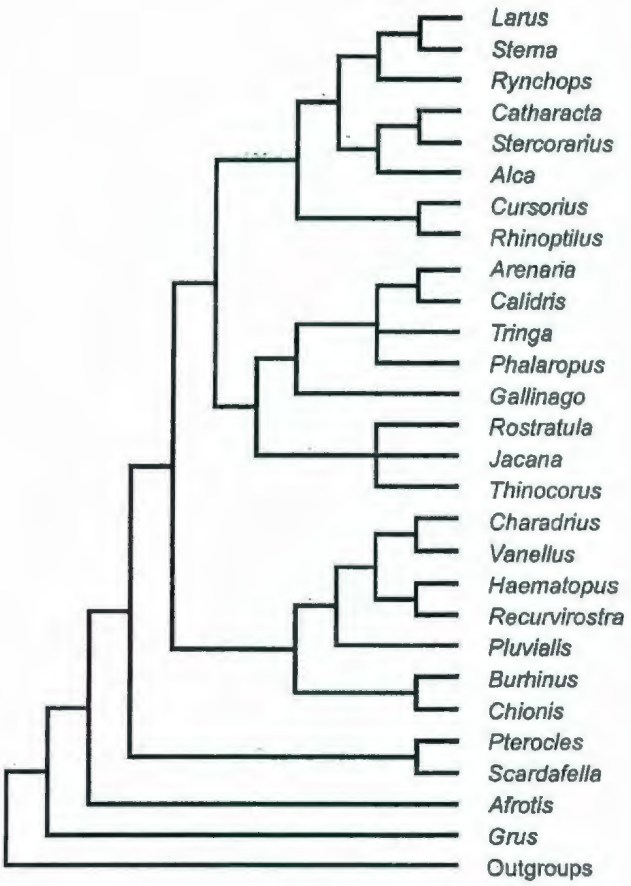
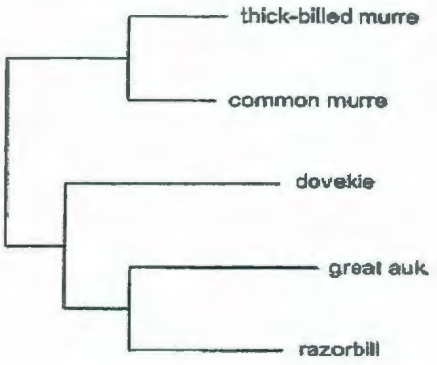


Figure 1.1. Phylogeny proposed by Ericson *et al.* (2003). Inter-familial relationships in charadriiformes based on nuclear DNA sequence data.

The Alcini is a clade of large black-and-white alcids composed of *Uria* (thick-billed murres, *U. lomvia* and common murre, *U. aalge) Alca* (razorbills, *Alca torda,* and the extinct great auk, *Penguinus impennis)* and *Alle* (dovekies, *Alle alle).* Their phylogenetic relationships (Moum *et al.* 2002) are:



The four extant Alcini species differ in modes of chick provisioning; murres deliver a single prey held longwise in the bill (single-loaders), razorbills deliver multiple prey held crosswise in the bill (multiple loaders), and dovekies transported food in a temporal pouch in the throat (internal transporters; Gaston & Jones 1998). These four species also differ on their breeding site charactheristics; murres breed on open nests, and razorbills (open nests as well) and dovekies breed on crevices (Gaston & Jones 1998). The longevity record for murres is 22-32 years and for razorbills 30 years (De Santo and Nelson 1995).

1.2 BACKGROUND OF STUDY

Decision-making about allocation of energy, time and risk is an ongoing task for animals during reproduction and it is believed that natural selection acts against individuals that fail to balance tradeoffs associated with these decisions. Furthermore, individuals are required to correctly allocate resources between current and future reproduction in order to maximize their fitness (Williams 1966). Balacing current and future costs and benefits of reproduction is particularly important for long-lived species such as seabirds (Stearns 1992), because excessive reproductive effort at one breeding attempt may greatly decrease individuals' lifetime reproductive success (Croxall & Rothery 1991; Woller *et al.* 1992).

Males and females do not necessarily raise offspring in perfect harmony because each individual should behave to maximize its own success even if this is at the expense of its mate (Trivers 1972). It has been suggested that females should usually be the care-giving sex because the costs of producing ova exceed those of sperm (Trivers 1972) and their progeny is limited by the number of eggs they produce (reproductive potential; Krebss & Davies 1991; Hall *et al.*1998). In contrast, assuming sperm is cheap, male's reproductive potential is virtually limitless, it seems likely that they can increase their reproductive success by mating with several females instead of investing in parental care (Hall *et al.*1998). These hypotheses seem to explain females' greater involvement in

parental care in some taxonomic groups with internal fertilization such as mammals, and birds with mixed-reproductive strategies (monogamous and polygamous). However, they failed to explain male post-zygote care in fish species with external fertilization and some bird species with polyandrous mating systems (Owens 2002). They also do not explain the dominant role that males play in raising chicks in socially monogamous species of Charadriiformes. For example, in scolopacids, females attend chicks for a shorter period after hatching than do males, and may even desert late in incubation (Gratto-Trevor 1991; Piersma 1996a; Payne & Pierce 2002). A similar but weaker trend also occurs in socially monogamous charadriids (Piersma 1996b).

About 90 % of avian species (100 % in seabirds) are socially monogamous (Lack 1968). In seabirds, biparental care is obligatory because a lapse of one parent's contribution leads inevitably to breeding failure. Both sexes need to balance their allocation towards offspring care and self-maintenance in response to changing demands of energy and time during reproduction (Drent & Daan 1980; Ydenberg *et al.* 1994). Thus, conflicting interests in the level of contribution between partners are likely to occur. Game theory models predict that only partial compensation for a mate's reduced parental effort must occur to maintain a stable evolutionary strategy of biparental care (Houston & Davies 1985; McNamara *et al.* 1999). Thus, males and females should compete to provide a minimum parental effort within a reproductive season to maximize their individual fitness. Handicapping experiments in birds have been able to measured the response of one member of the pair to the reduction of parental effot of the other

member by attaching weights to tail or by clipping feathers (Wright & Cuthill 1989; 1990; Whittingham *et al.* 1994; Markman *et al.* 1995; Sanz *et al.* 2000; Schwagmeyer *et al.* 2002). Some of these studies have found partial compensation for a partner's reduced effort (Wright & Cuthill 1989, 1990; Whittingham *et al.* 1994; Markman *et al.* 1995), supporting dynamic models, whereas others (Sanz *et al.* 2000) reported full compensation. Truly monogamous species such as seabirds are expected to be less likely to exploit their partners because maintaining their partners' condition enhances the fitness of both parents (Mock & Fujioka 1990; Fowler 1995). Thus, individuals of species with long-term pair bonds may distribute parental effort such that the partner who will benefit the most from contributing less parental effort does less work (K. M. Jones *et al.* 2002).

Although biparental care is necessary for success in seabirds, the level of contribution toward specific duties, or parental roles, may vary between sexes (Trivers 1972; Bart & Tornes 1989). The relative level of contribution may depend on life-history decisions of males and females in morphological, energetic, ecological and behavioural constraints during reproduction. Differences in parental roles between males and females have been found in several species of seabirds. Body size is the main factor to which these differences have been attributed in sexually dimorphic seabirds (Hamer & Furness 1993; Weimerskirch *et al.*, 2000). In sexually monomorphic seabirds (most species), sex differences in the form of parental care have been associated to competition for mates in sex-biased populations (Tershy & Croll 2000), differences in deferred maturity and mortality rates (Montevecchi & Kirkham 1981), different foraging strategies (Lewis *et al.*

2002), and ability to perform specific roles (Pierotti 1981; Furness 1983; Sproat & Ritchison 1993; Kis *et al.* 2000; Fraser *et al.* 2003).

In terms of functionality, animal's aggressive behaviour is used for self-protection and defence of mates, eggs and offspring (Archer 1998). The sexes are not expected to differ in levels of self-protection aggression unless there is a sex-biased predator pressure (Archer 1988). On the other hand, there is often specialization in defensive aggression by one sex (review by Archer 1988). Parental aggression in the form of offspring defence directly affects offspring survival and consequently the adult's fitness. Seabirds tend to be sexually monomorphic with biparental care of their young and as a result, sex differences in parental aggression are not expected. Nevertheless, male-biased aggressive behaviour has been reported in several seabird species. In some species, male aggressive behaviour appears to be driven by the need of defending the territory or the mates because it mainly occurs during the pre-laying and incubation periods (Spurr 1974; Morris & Bidochka 1982; Butler & Janes-Butler 1983; Moreno *et al.* 1995). However, males' aggressive behaviour and major role in nest defence persist through the chick-rearing period in many other seabird species (*Larus spp.*; Creelman & Storey 1980; Southern 1980; Burger 1981; Pierotti 1981) suggesting it may be driven by the need of protecting the offspring.

The members of the avian family Alcidae (Order Charadriiformes) are a diverse group of diving birds with remarkably variable forms of parental care and stages of chick development at the time of chick departure from the breeding site. At one end of the

spectrum, puffins (*Fratercula sp.*), guillemots (*Cepphus sp.*) and *Brachyramphus* murrelets provide biparental care at the nest site until chicks are nearly fully grown ("semi-precocial"; Sealy 1973) and fledge unaccompanied by their parents. At the other extreme, *Synthliboramphus* murrelets depart with their chicks two days after hatching ("precocial"; Sealy 1973), and both parents provide care at sea. In the tribe Alcini, thick-billed murres, common murres, and razorbills have a short period of biparental care at the breeding site (15-20 days) and partly grown chicks (15-30 % of adult body mass; "intermediate"; Sealy 1973) depart with the male parent to sea for an additional 3-4 weeks of exclusively paternal care (Gaston & Jones 1998). Tuck (1961) reported that collection of adult thick-billed murres accompanying chicks at sea indicated that either sex may care for the young at that age. Other studies has shown that the majority of birds taking the chick to sea (14/16 razorbills, Wanless and Harris 1986; 46/47murres, Bradstreet 1979) were males. The low occurrrence of females departing with the chick suggest it may be a result of accidental departure (i.e. gull disturbance). Partly grown dovekie chicks, the fourth extant Alcini member, also depart the colony with their male parent (27 days after hatching; Stempniewicz 1995; Harding *et al.* 2004), but with 68-72% of adult body mass ("semiprecocial", Sealy 1973, Norderhaug 1980; Stempniewicz 2001; Harding *et al.* 2004).

The most common explanation for the evolution of departure to sea of the partly-grown chicks of the Alcini tribe is the constraint on provisioning at the colony imposed by the load-carrying capacity (Houston *et al.* 1996; Gaston & Jones 1998). These large auks have the highest wing loading of all seabirds (Greenwalt 1962; Spear & Ainley

1997), which is a tradeoff for having excellent diving capacity. Consequently the flight costs of foraging and meal delivery are energetically expensive. However, this limitation should not apply so much to the much smaller planktivorous dovekies, and its applicability to razorbills that provision their chicks with multiple (sometime large) fish is questionable. Another explanation for early chick departure is that predation risk is high at the colony compared to at sea (Cody 1971; Ydenberg, 1989; Ydenberg *et al.* 1995). Ydenberg's (1989) model for the intermediate-fledgling alcids assumed that chicks have a lower mortality rate at the colony than at sea, but grow faster at sea than at the colony. Neither of these two assumptions are rigorously testable (i.e. logistical limitation) and more importantly, this 'tradeoff' hypothesis has no exclusive predictions (Gaston & Jones 1998). In this paper, I take as a starting point only that 'intermediate' chick colony departure is a phylogenetically fixed characteristic of the auk tribe Alcini.

Despite the different stages of development at chick departure, modes of chick provisioning, and nest-site characteristics (murres: open nests; razorbills: open and crevice nests; dovekies: crevice nests), the four Alcini members share a unique "intermediate" form of parental care; biparental care at the breeding site and uni-male parental care at sea. Two interesting questions that arise from patterns of parental care among the auk species are: How do the sexes allocate parental effort at the breeding site before paternal care begins when the chick departs the colony? and Why do males accompany chicks to sea?

Biparental care followed by male-only care also occur in other Charadriiformes such as Scolopaci (sandpipers, phalaropes) and Charadrii (plovers, lapwings, avocets).

In shorebirds, there are several hypotheses explaining why males care for the brood whereas the female desert at or early hatching. One explanation is the poorer condition of females because of the production of large eggs relative to their body size ("parental ability hypothesis"; Erckmann 1983). The Alcini species produce a single large and probably energetically costly egg (Birkhead and Nettleship 1982; 1984). In a review of the mechanisms underlying the costs of egg production, Williams (2005) conclude that females' investment in additional or larger eggs could potentially be recovered very rapidly during the post-laying period, or at least within the same breeding attempt, by increasing food intake. Measurements of body mass, body composition, and energetic costs during incubation in Kentish plovers (*Charadrius alexandrinus)* indicate no differential condition between sexes during incubation (Amat *et al.* 2000). Similarly, male and fermale common murres did not differ in body mass during late incubation and thorough the chick-rearing period (Wilhem 2004) suggesting that female poor condition may not explain male-only care. The "remating opportunity hypothesis"— females gain a greater reproductive success deserting than do males (Oring 1986) — is the best-supported explanation for the desertion of female in shorebirds with male-biased populations (Székely 1996; Székely *et al.* 2006).

Differences in energy expenditure due to different female-male constraints at the breeding site may cause one sex to be in better condition and thus better able to finish raising the chick at sea. For instance, different mortality rates (Nelson 1978), population ratios between sexes (Tershy & Croll 2000; Székely *et al.* 2006), foraging strategies (i.e.

self-provisioning and offspring feeding; Markman *et al.* 2004), and levels of aggressive behaviour (i.e. nest defense, Burger 1981; Fraser *et al.* 2002) are some factors that appear to affect the division of parental roles and effort allocation between sexes in biparental care species. Although both sexes guard their mates in an effort to assure paternity and to maintain pair bonds, extra-pair copulations and, to a lesser degree successful fertilizations occur in murres (thick-billed murres: Gaston & Hipfner 2000; common murres: review Ainley *et al.* 2002) and razorbills (Wagner 1992). Before egg-laying (3-4 weeks), males are continuously present at the breeding site (common murres) and/or mating arenas (razorbills) while female visitation is occasional (Gaston & Jones 1998). During this time males engage in fights for mate/site defense and are likely to fast or have reduced opportunities to feed (Birkhead *et al.* 1985), so overall they should have higher risk and energy costs than females. I hypothesized that sex-specific differences of murres and razorbills in contribution to parental care (effort allocation) at the time of departure may explain why males accompany chicks to sea. I expected parental care at the breeding site of both species to be mostly female-biased due to the male's initial expenditure of effort on mate guarding prior to egg-laying. I further expected that this would lead to males being in better condition than females at the time of departure to finish raising the chick at sea.

Thick-billed murres and razorbills are specialized wing-propelled divers that balance the demands for flying and diving (i.e., regulation of swimming speed; Lovvron *et al.* 1999). Both species spend considerably part of their time foraging at sea during

reproduction (Gaston & Jones 1998). Thus, the study of the foraging and diving behaviour of these alcids is an important component for the overall estimation of parental effort allocation between the sexes. For instance, breeding murres and razorbills feed their chicks with different prey taxa (i.e. fish) than those captured during the winter (i.e. crustaceans; Gaston & Hipfner 2000; Hipfner & Chapdelaine 2002, see also Rowe *et al.* 2000), which may reflect in their diving behaviour. Furthermore, incubating murres dived shallower than brooding murres probably due to different nutritional requirements for self-maintenance and chick provisioning (Benvenutti *et al.* 2002).

Thick-billed murre's diving behaviour has been extensively studied across their geographic range (Croll *et al.* 1992; Falk *et al.* 2000; Melhum *et al.* 2001; Watanuki *et al.* 2001; Benvenutti *et al.* 2002; Jones *et al.* 2002; Mori *et al.* 2002; Watanuki *et al.* 2006). They are generally deep divers and permormed mostly U-shaped dives when capturing prey (Croll et al.1992; Benvenutti *et al.* 2002). They feed on a variety of pelagic and benthic fish during reproduction (summer; see reviews by Gaston& Jones 1998; Gaston & Hipfner 2000) as well as invertebrates during non-breeding seasons (winter; e.g. Melhum 2001). In contrast, razorbills' diving behaviour has been much less studied (Benvenutti *et al.* 2001; Dall' Antonia *et al.* 2001; Watanuki *et al.* 2006). Razorbills are generally shallow divers (11-38 m), although they can dive as deep as 120 m (Piatt andNettleship1985).They perfomed mostly V-shaped dives (Benvenutti *et al.* 2001; Dall' Antonia *et al.* 2001)and feed on mid-water schooling fish (reviewed by Hipfner and Chapdelaine 2002). Only one study examined differences in diving behaviour between the sexes, and recorded that male thick-billed murres have longer

dives than females mainly due to differences in daily timing of foraging at Gannet Islands, Labrador (Jones *et al.* 2002).

Data loggers have been used extensively for the study of foraging behaviour of seabirds (Gales *et. al* 1990; Falk *et al.* 2000; Garthe *et al.* 2000; Mehlum *et al.* 2001; Shaffer *et al.* 2003). The attachment of external devices has shown to reduce swimming speed (Wilson *et al.* 1986), and increase hydrodynamic and aerodynamic drag during diving and flying (Bannash *et al.* 1994; Obrecht *et al.* 1988), which in turn increased energy expenditure and affected foraging performance (Wilson *et al.*1986; Gessaman & Nagy 1988; Croll *et al.* 1992; Culik *et al.* 1994). Seabirds with attached data loggers have been reported to have extended foraging trip durations (penguins: Croll *et al.* 1991; Watanuki *et al.* 1992; Hull 1997; Ropert-Coudert *et al.* 2000; Taylor *et al.* 2002; seals: Walker & Boveng 1995) and reduced nest visitation (alcids: Wanless *et al.*1988; Tremblay *et al.* 2003). Increase of workload due to instrumentation may be a special concern for large alcids, which have one of the highest wing loadings of any seabird species (Greenwalt 1962; Spear & Ainley 1997) as a trade-off of their excellent diving capacities. Therefore, it is important tocontrol for possible differential effects of instrumentation in the behaviour of male and female auks to be able to put the information in the context of parental effort allocation.

1.2 PURPOSE OF THE STUDY

This study examined sex differences in parental roles and diving behaviour of thick-billed murres and razorbills at Gannet Islands. The Gannet Islands Ecological Reserve protects the largest colony of razorbills (10,000 pairs) and the third largest colony of Atlantic puffins (38,000) in North America. The thick-billed murre population is considerably smaller than the common murre population (36,000 and 1,900 pairs respectively; Parks and Natural Division-Environment Canada).

My main objective was to quantify inter- and intra-specific patterns of parental care between sexes as attempt to understand why the male accompanies the chick to sea. Although a widespread tendency for paternal care late in chick rearing exists in Charadriiform birds (Gratto-Trevor 1991; Piersma 1996a; Piersma 1996b; Payne & Pierce 2002), it is relatively rare among the alcids (4 of 23 extant species). Thus, my approach was to identify characteristics of two alcid species that could favour such a pattern. Although murres and razorbills share similar life-history strategies, they also differ in many aspects of their foraging ecology (Gaston & Jones 1998). Therefore, it is unclear how two sister-species segregate in the light of niche-partitioning concepts when capturing prey. My second objective was to determine whether the sexes of two sympatric diving species differ in their foraging strategies particularly in their behaviour underwater.

In chapter two, I quantify the effect of external time-depth recorders on body condition and parental behaviour (brooding time and provisioning rates) of female and male thick-billed murres rearing chicks. Secondly, I examine whether the partner of a TDR-equipped bird would compensate for a reduction in parental effort by a gear-encumbered mate and whether this behaviour was sex biased. In addition, I measure post-effects of TDR deployment on return rates, breeding success and mate fidelity. This chapter was published in *Animal Behaviour* (2004) jointly with Dr. Ian Jones and Dr. Daryl Boness.

In chapter three, I examined sex differences in diving behaviour and diet in thick-billed murres and razorbills. I specifically analyzed time of day effects on dive and bout parameters and compared dive profiles (shapes and parameters) between the sexes in each species. This dive information was related to their main prey taxa captured for chick provisioning. This chapter is in review for publication in *Canadian Journal of Zoology* (2008) jointly with Dr. Ian Jones, Dr. Daryl Boness, Dr. Yann Tremblay and Dr. Martin Renner.

In chapter four, I investigated whether parental roles of male and female thick-billed murres reflect different foraging strategies for self-feeding and chick provisioning. It was possible to distinguish between the two foraging activities because murres perform a direct flight back to the colony for chick provisioning. I specifically measured dive parameters and foraging trip durations for each category, and estimated distance to

foraging areas by using combined information of time-depth recorders and observations at the breeding site.

In chapter five, I analyzed differences in aggressive behaviour between the sexes in both auk species during the incubation and brooding period. I studied the aggressive behaviour of the on-duty parent in the absence of its mate in order to ensure that the aggression was directed toward the protection of the egg/offspring instead of the mate. I measured aggressive responses of attending individuals (egg/chick) in two different conditions: a) opportunistic observations of aggressive interactions between con- and heterospecifics; and b) experimental observations of aggressive behaviour resulting from the presentation of a model predator. This chapter was submitted jointly with Dr. Stephen J. Insley for publication in *Ibis* (2008).

In the sixth chapter, I sum up the ways male and female of both alcid species differed in their parental roles at the breeding site. I examined four components of parental care: breeding site attendance (egg/chick care and breeding site defence), provisioning rates, prey size delivered to chicks, and foraging trips. In this final chapter, I combine the results from this and previous chapters to discuss the differential energy expenditure hypothesis proposed to explain the occurrence of male-only care in murres and razorbills. This chapter has been published, jointly with Dr. Ian Jones and Daryl Boness, in *Behaviour*.

1.2 SIGNIFICANCE OF THE STUDY

Understanding how males and females distribute parental roles may give us insights into how evolution has shaped forms of parental care, the extent to which morphological, physiological and behavioural factors limit the allocation of parental effort, and why the transition to paternal care at sea occurs in the first place. The detailed study of the parental roles in sister auk species with similar chick-rearing strategies can help to undertand the mechanisms driven differences in foraging behaviour between males and females.

CO-AUTHORSHIP STATEMENT

I have made a major intellectual and practical contribution to all work that is reported in my thesis. I am the principal author of all the manuscripts that had been published or submitted to peer-review journals. Specifically, i) I have made the design and identification of the research proposal with advice of my supervisor, Dr. Ian Jones. ii) I organized all aspects of the research such as, writing of proposals for funding (e.g. research assistants, equipment) and required permits to work at Gannet Islands (e.g. CWS, Animal Care); and purchasing of field equipment. I also perfomed most bird manipulations (e.g. captures and deployment of data loggers), and data collection. My assistants followed a detailed protocol I wrote for all activities we undertook in the field. iii) I performed all data analysis, except for the initial part of dive analysis (i.e. generation of dive parameters) that was done in Y. Tremblay's program. iv) I had the lead role in the preparation of all manuscripts, which were benefited with the comments of co-authors and supervisory committee members.

CHAPTER 2: REDUCED PARENTAL CARE, COMPENSATORY BEHAVIOUR AND REPRODUCTIVE COSTS EXPERIENCED BY FEMALE AND MALE THICK-BILLED MURRES EQUIPPED WITH DATA LOGGERS

2.1 ABSTRACT

Theoretical models predict that in species with obligate biparental care, individuals will partially compensate for decreased parental effort by their partners as a stable evolutionary strategy. Full compensation may occur when breeding success is an accelerating function of parental effort, especially in long-lived bird species. I experimentally examined the effect of time-depth recorders (TDRs) on body mass and parental behaviour of thick-billed murres *Uria lomvia*, and evaluated the effect of TDRs as handicaps to test whether there was compensation for decreased partner effort and whether this behaviour was sex biased. Compared with control birds, TDR-equipped birds had reduced body mass, offspring attendance, number of foraging trips and feeding rates, and males had increased foraging trip duration. In general, males lost mass at higher rate and made longer foraging trips than females. Partners of TDR-equipped birds compensated for their mates' reduced parental effort by increasing offspring attendance

and by increasing chick provisioning above averages rates of control birds. Although partners of TDR-equipped birds fully compensate for their mates' reduced offspring attendance (i.e. chicks were never observed to be left unattended), total provisioning rates of pairs with a TDR-equipped bird (mean ± SE: 4.38 ± 0.26 meals day $^{-1}$) were significantly lower than those of control birds (mean ± SE: 5.74 ± 0.31 meals day $^{-1}$). However, fledgling success of control and TDR-equipped birds did not differ between reproductive seasons. TDR-equipped birds also had a significantly lower rate of return to breed than their non-equipped partners or control birds, and those that did return the following season were more likely to change mates (32%) compared with controls (0%). Taken together, my results underline the need to quantify the effects of monitoring equipment used to measure seabird's activities, and indicate the ability of female and male thick-billed murres to compensate for reduced partner effort due to handicapping. Compensatory behaviour seems to be a necessary response of this single-brooded species to ensure current breeding success; however it may affect the stability of pair bonds in some individuals.

2.2 INTRODUCTION

According to life-history theory, animals will tend to minimize their effort during current reproduction to maximize survival and lifetime reproductive success (Williams 1966).

In species with biparental care, both parents need to balance their allocation towards offspring care and self-maintenance in response to changing demands of energy and time during reproduction (Drent & Daan 1980; Ydenberg *et al.* 1994). Thus, conflicting interests in the level of contribution between partners are likely to occur. Game theory models predict that only partial compensation for a mate's reduced parental effort must occur to maintain a stable evolutionary strategy of biparental care (Houston & Davies 1985; McNamara *et al.* 1999). Thus, males and females should compete to provide a minimum parental effort within a reproductive season to maximize their individual fitness.

Empirical studies have tested these predictions using mate removal, testosterone implants, and handicapping experiments in monogamous species. Mate removal studies have provided insights to the function of biparental care and monogamy across different taxa (birds: Bart & Tornes 1989; review of male-removal by Moller *et al.* 2000; Transue & Burger 1989; beetles: Fetherston *et al.* 1994; Hunt & Simons 2002; and fish: Mrowka 1982; Lavery & Reebs 1994); and showed that individuals' response to the loss of their mates varies from abandonment to complete compensation of parental effort. Nevertheless, these experiments have failed to test dynamic models of bargaining of parental effort between males and females. Although experiments with testosterone implants (e.g. Saino & Moller 1995; Hunt *et al.* 1999; Alonzo-Alvarez 2001) have been used to reduce paternal effort, female compensation is difficult to interpret because a female's behaviour can be affected by the endocrine manipulation of her partner (Alonzo-

Alvarez 2001). Handicapping experiments using birds have reduced parental effort of one member of the pair by attaching weights to tail or clipping feathers (Wright & Cuthill 1989, 1990; Whittingham *et al.* 1994; Markman *et al.* 1995; Sanz *et al.* 2000; Schwagmeyer *et al.* 2002), so the level of response of the other member can be measured. Some of these studies have found partial compensation for a partner's reduced effort (Wright & Cuthill 1989, 1990; Whittingham *et al.* 1994; Markman *et al.* 1995), supporting dynamic models, whereas others (Sanz *et al.* 2000) reported full compensation. A recent model of biparental care has proposed that full compensation may occur when the breeding success is an accelerating function of parental effort, i.e., in species with high predation levels, high breeding density or poor condition of one parent (Jones *et al.* 2002b). Other studies have found a lack of compensation for reduced partner effort (Slagsvold *et al.* 1990; Saether *et al.* 1993; Schwagmeyer *et al.* 2002). Overall, these results suggest that further studies are required to better understand the dynamic of bargaining of effort levels between sexes.

Most handicapping experiments testing for compensatory behaviour have been performed in socially monogamous passerines and used chick feeding as the only measure of parental care (but see Markman *et al.* 1995); only one has been reported for a seabird (Saether *et al.* 1993). Long-lived seabirds are thought to be less likely to increase their investment in a current reproduction and risk affecting their future breeding (Curio *et al.* 1988; Pugesek & Diem 1990). On the other hand, seabird's responses to reduced parental effort due to handicapping may be easier to interpret because confounding

variables common in passerines, such as frequent extra-pair copulations and multiple broods, are rare or absent.

Data loggers have been used extensively for the study of foraging behaviour of seabirds (e.g. penguins' review in Gales *et. al* 1990; Falk *et al.* 2000; Garthe *et al.* 2000; Mehlum *et al.* 2001; Shaffer *et al.* 2003), pinnipeds (e.g. Kooyman *et al.* 1976; Boness *et al.* 1994; Hooker *et al.* 2002), cetaceans (e.g. Ray *et al.* 1978; Frost *et al.* 1985; Croll *et al.* 2001), and turtles (e.g. Eckert *et al.* 1989; Minamikawa 2001). The attachment of external devices has been shown to reduce swimming speed (Wilson *et al.* 1986), and increase hydrodynamic and aerodynamic drag during diving and flying (Obrecht *et al.* 1988; Bannash *et al.* 1994), which in turn increased energy expenditure and affected foraging performance (Wilson *et al.*1986; Gessaman & Nagy 1988; Croll *et al.* 1992; Culik *et al.* 1994). Although few studies have tested the effect of such devices on parental performance using equipped and non-equipped animals, extended foraging trip durations have been reported in several species of penguins (Croll *et al.* 1991; Watanuki *et al.* 1992; Hull 1997; Ropert-Coudert *et al.* 2000; Taylor *et al.* 2002; but see Gales *et al.* 1990; Ballard *et al.* 2001) and in the Antarctic fur seals (*Arctocephalus gazella*, Walker & Boveng 1995). In flying seabirds, reduced nest visitation has been reported for alcids carrying radio-transmitters with external antennas (Wanless *et al.*1988) or time-depth recorders (Tremblay *et al.* 2003); but no effects have been found in king cormorants (*Phalacrocorax albiventer*, Kato *et al.* 2000) and wandering albatrosses (*Diomedea*

exulans, Schaffer *et al.* 2003). Thus, data loggers can be used as handicapping tools in species where they increase breeding effort.

Increase of workload due to instrumentation may be a special concern for large alcids, which have one of the highest wing loadings of any seabird species (Greenwalt 1962; Spear & Ainley 1997) as a tradeoff of their excellent diving capacities. In fact, the intermediate chick development strategy shared by thick-billed murres, common murres, *Uria algae*, and razorbills, *Alca torda* has been attributed to reduce high costs of chick provisioning at the breeding site (Gaston & Jones 1998).

This study had two main objectives; one was to quantify the effect of external time-depth recorders on body condition and parental behaviour of female and male thick-billed murres rearing chicks. The second objective, which could only be fulfilled if the recorders handicapped the birds on which they were deployed, was to determine whether the partner of a TDR-equipped bird would compensate for a reduction in parental effort by a gear-encumbered mate and whether this behaviour was sex biased. I used brooding time and provisioning rates as estimates of parental care. In addition, post-effects on return rates, breeding success and mate fidelity were examined.

2.3 METHODS

I studied thick-billed murres at island GC4, one of the six Gannet Islands on the low-arctic coast of southern Labrador, Canada (53°56'N, 56°32'W), and a colony of about 150 pairs. A total of 62 pairs were followed during the brooding periods (June-August) for 2000, 2001, 2002 and 2003. Of these, 18 males and 22 females (one mate per pair) rearing chicks were captured for attachment of time-depth recorders. Both of the TDR types used, MK7 (Wildlife Computers, Redmond Washington, U.S.A.; 25 g, flat shape with pointed end) and LTD_100 (Lotek Marine Technologhy, St. John's Newfoundland, Canada; 16 g, cylindrical shape with rounded end) were similar in size (5–8 x 1–2 x 1–2 cm), and in cross-sectional area (1.7–1.9 cm^2, 1.2–1.3 % of the body area). Birds were captured using noose poles from the edge of the cliff above the colony. After capture, each bird's mass was measured to the nearest 10 g using a spring scale and individuals were marked with permanent (stainless steel) and temporary (color) numbered bands. TDRs were attached to the back of feathers using three strips of black TESA tape, cable ties and drops of cyanoacrylate glue ("hot stuff"®) under both ends of the device. TDRs were placed on backs of birds to maintain their centre of gravity (Kenward 1987) and balance the total mass during flying (Obrecht *et al.* 1988). Birds preened their dorsal feathers so part of the frontal and lateral edges of the device were covered by contour feathers, which may help to reduce drag during swimming (Bannash *et al.* 1994). In addition, the color of tape used resembled bird's plumage color, which seems to reduce

the frequency of pecking (Wilson *et al.* 1990). Handling time from capture to release totaled between 5–8 minutes. Birds were re-captured after 1– 4 days for TDR recovery and re-weighed. Blood samples (0.5 ml) were taken from the tarsus vein and stored in vials with 95% ethanol for use later for sex determination by molecular DNA analysis (Fridolfsson *et al.* 1999). During capture and re-capture both adults were present at the breeding site so chicks were never left alone. This procedure was used to ensure chick safety and to reduce possible stress on captured birds that would have been caused by leaving their offspring unattended.

To quantify parental care of murres equipped with TDRs (16 males and 19 females) and their partners, observations were undertaken before and after TDR deployment, and after TDR removal during 2000 and 2001. The same information was obtained simultaneously for a group of undisturbed birds without TDRs (control birds: 13 females, 13 males). Both groups of birds had chicks of similar ages, ranging from 1 to 15 days old. Behavioural observations were undertaken from a blind using binoculars and a zoom telescope between dawn and dusk (0400 – 2200 h) during 3–15 days of the chick-rearing period. Breeding sites were scanned every 10 minutes and the presence/absence and identity of adults were recorded to calculate the time spent at the breeding site per day. The departure and arrival of adults and chick provisioning events were recorded continuously to calculate feeding frequencies and foraging trip durations. In order to be able to identify individuals before capture, I temporarily marked birds with picric acid (yellow) or fluorescent paint (green, pink and orange). I attached a small container (10 cc

of marking liquid) to the tip of the noose pole so drops of the liquid could be delivered from above the birds without disturbing the colony. Birds were marked as if they were hit by falling guano, which is a normal occurrence in the colony, so disturbance caused by marking was minimal. The mark patterns, along with other life history information were recorded on ID cards for quick reference. Non-equipped birds were captured twice (4–17 day interval) and manipulated during a similar time period to the TDR-equipped birds to determine rates of mass loss. These were marked with a field readable stainless steel leg band and a color band, and a blood sample was taken for sex determination (Fridolfsson *et al.* 1999). The results of sexing were obtained after the season was finished (observers were blind to the sex of birds) and then matched with the ID cards to interpret behavioural data.

A total of 30–43 pairs of non-equipped birds at breeding sites were checked daily from hatching to fledging to quantify fledging success. The fledging success of TDR-equipped and control birds was measured during the current (all years) and following breeding season. A sub-sample of control, TDR-equipped birds and their partners, individually marked with color bands, were monitored during the following breeding season to measure subsequent return rates, and maintenance of pair bonds. Return rate was calculated based on the birds that were present at the colony during incubation and brooding. I did not perform observations before the laying period.

2.3.1 Data analysis

To determine the effects of TDRs on body condition (mass loss) and parental behaviour (chick attendance, number and duration of foraging trips, feeding rates) data were compared between groups (control and TDR-equipped birds) and sexes. Measures of parental behaviour for individuals were averaged per day, and comparisons between groups were undertaken using the same chick ages (up to 11 days). In order to quantify feeding compensation by partners I first did a cross-sectional analysis of chick provisioning rates between three groups (TDR-equipped birds, their partners and control birds), and also between sexes. Then, I did a longitudinal analysis of TDR-equipped birds and their partners to account for possible individual differences between groups. Matched-pair comparisons of chick provisioning rates of TDR-equipped birds, their partners and the pair (both parents) were made before the TDR was deployed (before TDR) and after it was deployed (TDR deployed). In addition, paired comparisons were made between the two previous stage categories (before TDR and TDR deployed) and after TDR removal (TDR removed) to determine possible differences in chick provisioning and compensatory behaviour. For the consistency of the analysis I sampled the same number of days each bird was equipped with the TDR (1-4 days) to calculate the average provisioning rates before TDR deployment and after TDR removal. Finally, in order to compare the total chick provisioning between control pairs and pairs with a TDR-equipped birds (Pair TDR-equipped bird), I matched chick ages to the three

deployment stages, before TDR (up to 7 days), TDR deployed (4-11 days) and TDR removed (12-15 days).

For each individual, I calculated time spent at the breeding site per 24 hr even though the observation period only covered the daylight hours (18 hr). Previous studies have shown that thick-billed murres at the Gannet Islands do not make changes at night (Jones *et al.* 2002a). In this study, the same bird present at dusk was found the following morning with a dirty plumage, suggesting it did not leave the breeding site during the night. So I added six hours (dark time) to the observed time the bird spent at the breeding site during the day.

Analysis of foraging trips included trips with and without a fish delivered to a chick. It was not possible to distinguish between bathing trips and feeding trips because birds could return to the breeding site with a fish after absences of less than 10 min. The first foraging trip was usually performed by females, which normally spent the night at sea (Jones *et al.* 2002a) and arrived at the breeding site in the early morning. Thus, in order to calculate the duration of the first foraging trip I assumed birds started to forage right after sunrise (0330 h). Chick provisioning was calculated as the number of meals per individual and per pair per day.

Statistical analysis was carried out using SPSS version 11.5. I used parametric tests (Student's *t* test, ANOVA, and Paired *t* test) to compare groups if the residuals met

the assumptions for the general linear model (homogeneity and normality). I report 95% confidence intervals instead of estimates of statistical power to address the question of Type II error (Hoenig & Heisey 2001). Multiple comparisons were undertaken using the Post-hoc Tukey HSD test. The Chi-square test was used to compare two categorical proportions. Means were expressed ± SE of the mean. All comparisons were two-tailed, except otherwise, and differences were considered significant when $P < 0.05$.

2.4 RESULTS

2.4.1 Inter-annual fledging success

The fledging success of thick-billed murres was high and did not differ among years (2000: 0.93 fledglings breeding site $^{-1}$, $N = 30$; 2001: 0.98 fledglings breeding site^{-1}, $N = 40$; 2002: 0.98 fledglings breeding site^{-1}, $N = 43$; ANOVA: $F_{1, 112} = 0.576$, $P = 0.564$). Based on these results, data were pooled for the analysis of mass loss (2000–2002) and parental care (2000–2001).

2.4.2 Effect of time-depth recorders on body mass and parental behaviour

2.4.2.1 *Effect on body mass*

The initial body mass of males (965 ± 10 g, $N = 32$) was higher than females (917 ± 9 g, $N = 37$; ANOVA: $F_{1, 67} = 13.01$, $P = 0.001$), and it did not differ between control (948 ± 10 g, $N = 31$) and TDR-equipped birds (932 ± 10 g, $N = 38$; ANOVA: $F_{1, 67} = 1.347$, $P = 0.25$). The relative mass of the TDR to initial body mass was on average 2.7 % and 2.4 % for females and males respectively. The rate of mass loss varied between control and TDR-equipped birds (ANOVA: $F_{1, 63} = 75.77$, $P < 0.0001$) and with sex ($F_{1, 63} = 4.93$, $P = 0.030$); and the interactive effect of the factors on mass loss was significant ($F_{1, 63} = 4.84$, $P = 0.031$). Further analysis of the main factors showed that mass loss rates were significantly higher on TDR-equipped males (-27.01 ± 3.02 g day $^{-1}$, $N = 15$) and TDR equipped females (-18.15 ± 2.54 g day $^{-1}$, $N = 21$) than control males (-3.98 ± 0.64 g day $^{-1}$, $N = 15$; ANOVA: $F_{1, 28} = 59.45$, $P < 0.0001$) and control females (-3.94 ± 0.95 g day $^{-1}$, $N = 16$; ANOVA: $F_{1, 35} = 21.88$, $P < 0.0001$) respectively. TDR-equipped males lost mass at a higher rate than TDR-equipped females (ANOVA: $F_{1, 34} = 5.988$, $P = 0.020$), and within control birds both sexes lost weight at a similar rate (males: -3.98 ± 0.64 g day $^{-1}$, $N = 15$; females: -3.94 ± 0.95 g day $^{-1}$, $N = 16$; ANOVA: $F_{1, 29} = 0.002$, $P = 0.97$). Similar results were obtained when controlling for the initial mass of each bird. The mass loss ratio varied between groups (ANOVA: $F_{1, 63} = 73.01$, $P < 0.0001$) and sexes ($F_{1, 63} = 4.013$, $P = 0.049$). The interactive effect of the factors on mass loss ratio was

significant ($F_{1, 36} = 4.145$, $P = 0.046$). In both sexes, TDR-equipped birds had significantly higher mass loss ratios than control birds (ANOVA: females- $F_{1, 35} = 23.41$, $P < 0.0001$, males- $F_{1, 28} = 63.05$, $P < 0.0001$). Within groups, differences between sexes were only significant within TDR-equipped birds, with males losing proportionately more than females relative to their body mass (ANOVA: $F_{1, 34} = 5.018$, $P = 0.032$, Figure 2.1).

Four of the TDR-equipped birds that were still brooding chicks (2 males and 2 females) were re-weighed 7-14 days after the TDRs were removed. All birds, except for one female (-3.5 g day $^{-1}$), increased in mass (4.2 ± 0.4 g day $^{-1}$) after TDR removal.

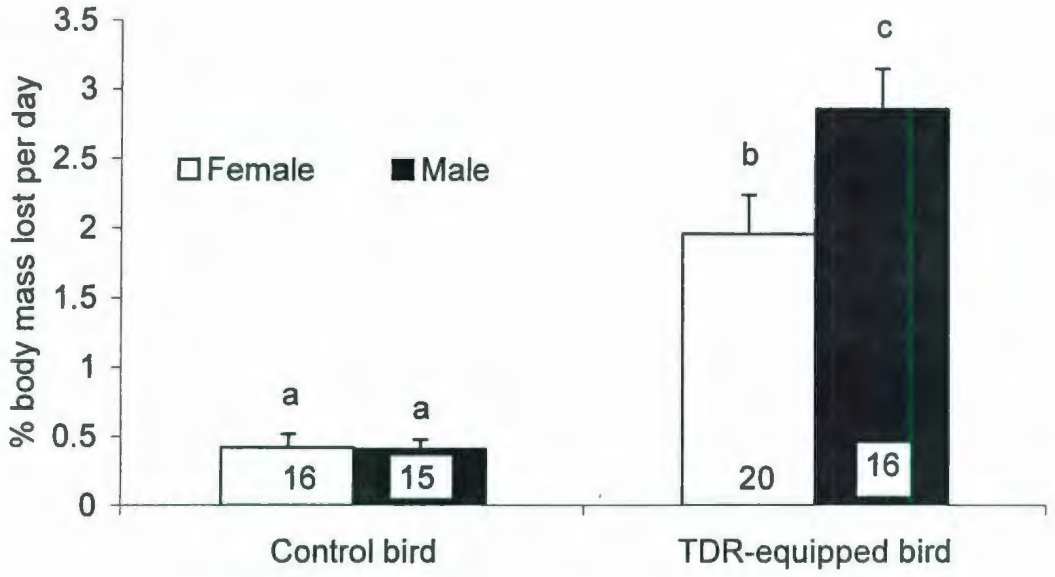


Figure 2.1 Mass loss (mass loss per body mass per day) of control and TDR-equipped thick-billed murres rearing chicks at the Gannet Islands, Labrador. Means ± SE. Different letters above bars denote statistical differences between groups (ANOVA, $P < 0.0001$). For example, control females (a) differ from TDR-equipped females (b) but not from control males (a).

2.4.2.2 *Effect on foraging behaviour*

Thick-billed murres performed 1 to 12 foraging trips per day, lasting between 10 and 720 minutes. Parents delivered one to six fish to their chicks per day. Males foraged mostly during the day (0600 –1500) and females before sunset (2200 h) and after sunrise (0330 h).

Individual provisioning rates of control pairs and pairs with a TDR-equipped member (with chicks up to 7 days old) were compared before TDRs were deployed to check for possible individual differences between groups. I found no significant interactive effect of the group and sex on chick provisioning (ANOVA: $F_{1, 114} = 0.083$, $P = 0.774$). Provisioning rates did not differ significantly between groups (control pairs: 2.46 ± 0.18 meals individual $^{-1}$day $^{-1}$, $N = 26$; pairs with a TDR-equipped bird: 2.21 ± 0.12 meals individual $^{-1}$day $^{-1}$, $N = 35$; ANOVA: $F_{1, 114} = 1.437$, $P = 0.233$), or sexes (females: 2.22 ± 0.14 meals individual $^{-1}$day $^{-1}$, $N = 32$; males: 2.41 ± 0.15 meals individual $^{-1}$day $^{-1}$, $N = 26$; $F_{1, 114} = 0.755$, $P = 0.387$). The mean values of both groups (control and equipped birds) and sexes were within the 95% confidence limits (2.13 - 2.54 meals day $^{-1}$) of the grand mean.

To examine the effect of TDRs on chick provisioning, chick attendance, and number and duration of foraging trips, I compared the mean rates of control (13 males and 13 females) and TRD-equipped birds (16 males and 19 females) using the same chick age categories (up to 11 days old). Provisioning rates of TDR-equipped birds were less than half of control birds (ANOVA: $F_{1, 57} = 70.33$, $P < 0.0001$). There was no difference in provisioning rates between sexes ($F_{1, 57} = 0.151$, $P = 0.699$) nor was there an interaction between instrument status and sex ($F_{1, 57} = 0.295$, $P = 0.589$, Table 2.1). In control pairs, males and females did not differ significantly on their mean provisioning rates (ANOVA, $F_{1, 25} = 1.012$, $P = 0.324$, Table 2.1).

Both male and female TDR-equipped birds performed fewer foraging trips per day than control birds (Table 2.1; ANOVA: TDR condition- $F_{1, 57} = 67.46$, $P < 0.0001$; sex - $F_{1, 57} = 0.187$, $P = 0.667$). No interactive effect of the factors on foraging trip was detected ($F_{1, 57} = 0.700$, $P = 0.406$).

Foraging trip duration varied between groups (ANOVA log-data transformed: $F_{1, 57} = 13.74$, $P < 0.0001$) and sexes ($F_{1, 57} = 36.91$, $P < 0.0001$, Table 2.1). There was not a significant interaction effect of group*sex on trip duration (ANOVA: $F_{1, 57} = 3.263$, $P = 0.076$). Further analysis of the main factors was done due to the small P value of the interaction term. Within sexes, TDR-equipped males performed longer foraging trips than control males (ANOVA: $F_{1, 27} = 15.498$, $P = 0.001$). However, the trip duration did not differ between TDR-equipped females and control females ($F_{1, 32} = 2.694$, $P = 0.111$). In both groups, males performed longer foraging trips than females (ANOVA: control- $F_{1, 24} = 14.90$, $P = 0.001$; TDR condition- $F_{1, 33} = 23.92$, $P = 0.0001$).

Table 2.1. Effect of externally attached time-depth recorders on parental behaviour of female and male thick-billed murres rearing chicks at the Gannet Islands, Labrador.

	Control birds			TDR-equipped birds		
	Females	Males	Pooled	Females	Males	Pooled
Meals per day	2.7 ± 0.27	2.5 ± 0.24	2.6 ± 0.18*	0.9 ± 0.13	0.9 ± 0.22	0.9 ± 0.12*
Foraging trips/day	4.0 ± 0.27	3.7 ± 0.29	3.8 ± 0.20*	1.9 ± 0.17	2.0 ± 0.22	1.9 ± 0.13*
Trip duration (h)[1]	1.4 ± 0.37	2.2 ± 0.39*	1.8 ± 0.29*	1.8 ± 0.48	4.6 ± 0.49*	2.8 ± 0.35*
Chick attendance (h)	9.9 ± 0.28	14.5 ± 0.30*	12.2 ± 0.52*	8.9 ± 0.36	12.3 ± 0.86*	10.5 ± 0.52*

Means are given ± SE. Comparisons were done between groups (pooled data) and sexes (males and females) within each group. Significant differences between control (N = 13 females, 13 males) and TDR-equipped birds (N = 19 females, 16 males) and sexes are shown.

*Two-way ANOVAs, $P \leq 0.001$.

[1]Data were log (base 10)-transformed before the statistical analysis.

2.4.2.3 *Effect on brooding behaviour*

Parents attended their breeding sites alternately during the chick rearing period, which lasted 15–24 days. Most females brooded their chicks from early morning to late afternoon (overnight at sea) and males from late afternoon until the next morning (overnight at the breeding site). The duration of the chick raising period did not differ significantly between pairs with a TDR-equipped member (20.69 ± 0.43 days) and control pairs (21.15 ± 0.54 days; Student's *t* test: $t_{37} = -0.643$, $P = 0.524$). The means of both groups were within the 95% confidence limits (20.17 – 21.54 days) of the grand mean.

Birds equipped with TDRs spent less time brooding their chicks than control birds (ANOVA: $F_{1, 57} = 9.959$, $P = 0.003$). Overall males stayed with the chick proportionately more than females for both groups (Table 2.1; ANOVA: $F_{1, 57} = 52.07$, $P < 0.0001$). There was no significant interaction between group and sex on the brooding time ($F_{1, 57} = 1.375$, $P = 0.246$). Within sexes, TDR-equipped males spent significantly less time brooding than control males (ANOVA: $F_{1, 57} = 4.893$, $P = 0.036$). On average TDR-equipped females stayed with the chick less time than control females, however these differences were not significant ($F_{1, 57} = 3.491$, $P = 0.071$).

2.4.3 Compensation of reduction of parental effort

2.4.3.1 *Chick provisioning*

I compared chick provisioning rates among three groups (TDR-equipped birds, partners of TDR-equipped birds and control birds), controlling for possible sex differences, to determine whether partners would compensate for reduced parental effort by TDR-equipped birds. Provisioning rates differed significantly by group ($F_{2, 136} = 37.99$, $P < 0.0001$), but not by sex ($F_{1, 136} = 0.454$, $P = 0.502$, Figure 2.2); and there was no interactive effect of the factors on the response variable ($F_{2, 136} = 1.149$, $P = 0.320$). Partners of TDR-equipped birds (3.42 ± 0.25 meals day $^{-1}$) fed chicks at a significantly higher rate than TDR-equipped birds (0.87 ± 0.12 meals day $^{-1}$) or control birds (2.60 ± 0.15 meals day $^{-1}$, Tukey HSD test: $P < 0.004$, Figure 2.2). Comparisons of provisioning rates between the partners of TDR-equipped birds and control birds revealed that male partners had higher rates than male control birds (ANOVA: $F_{1, 52} = 10.70$, $P < 0.002$), but female partners did not differ from those of control females ($F_{1, 54} = 0.954$, $P = 0.333$; Figure 2.2). However, the longitudinal analysis of pairs with a TDR equipped birds (see below) showed that partners of both sexes increased their provisioning rates after TDR deployment.

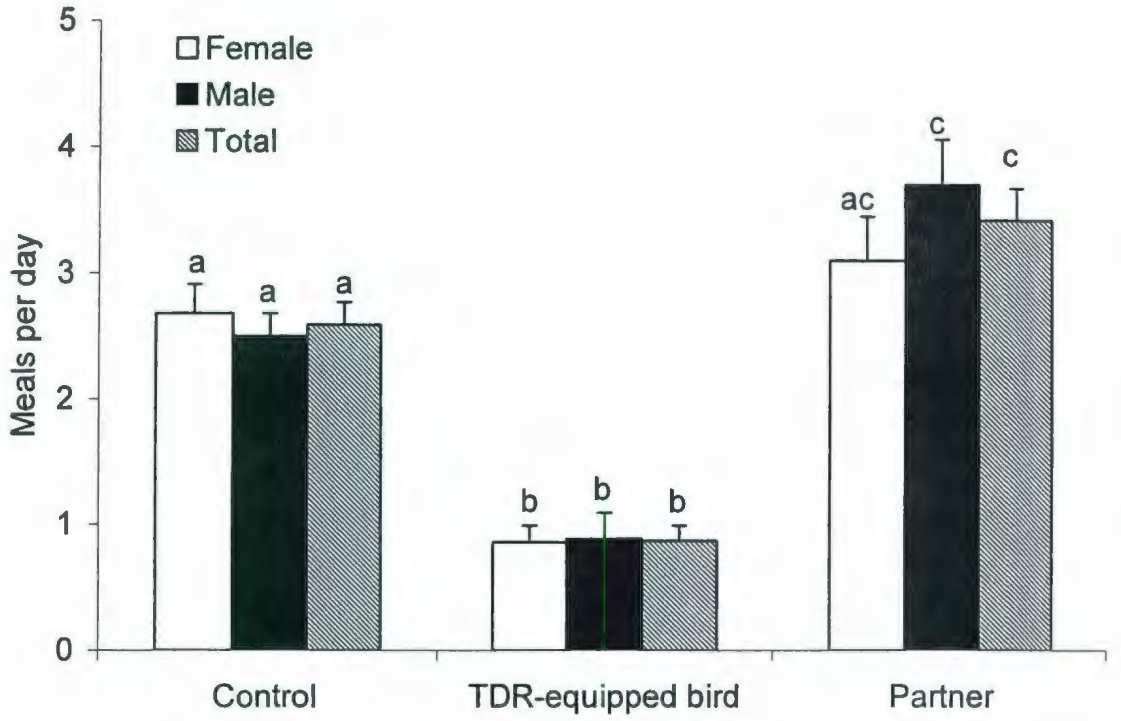


Figure 2.2 Overall effect of TDR deployment on chick provisioning in thick-billed murres at the Gannet Islands, Labrador. Data show feeding rates (mean ± SE) of TDR-equipped birds (19 females, 16 males), their partners and control birds (13 females, 13 males). Different letters above bars denote statistical differences between groups (two-way ANOVA, $P < 0.0001$). For example, control female (a) differ from TDR-equipped female (b) but not from partner female (ac).

In order to account for possible individual differences among pairs with a TDR-equipped member and control pairs, I used a longitudinal analysis to examine the effect of TDR deployment on chick provisioning. Paired *t*-test comparisons before and after TDR deployment were made on 24 pairs of TDR-equipped birds and partners. The TDR-equipped birds reduced their provisioning rates after TDRs were deployed (Paired *t* test: *t*

$_{23} = 8.549$, $P < 0.0001$), whereas their unencumbered mates increased their rates significantly (before: 2.19 ± 0.25 meals day $^{-1}$, after: 3.55 ± 0.31 meals day $^{-1}$; $t_{23} = -4.084$, $P < 0.0001$). For partners of TDR-equipped birds, both males (before: 2.51 ± 0.43 meals day $^{-1}$, after: 3.83 ± 0.44 meals day $^{-1}$; Paired t test: $t_{11} = -3.058$, $P = 0.011$) and females (before: 1.86 ± 0.26 meals day $^{-1}$, after: 3.26 ± 0.43 meals day $^{-1}$; Paired t test: $t_{11} = -2.661$, $P = 0.022$) increased their feeding rates significantly after TDR deployment.

A similar approach was used to determine whether chick provisioning rates of TDR-equipped birds or of their partners changed after the TDR was removed. The mean provisioning rates of previously TDR-equipped birds increased significantly (Paired t test: $t_{19} = -4.37$, $P = 0.001$, Figure 2.3) to values similar to before the TDR deployment (Paired t test: $t_{19} = 1.35$, $P = 0.194$). Their partners maintained provisioning rates (Paired t test: $t_{19} = 0.31$, $P = 0.79$), which were significantly higher than those before the TDR deployment (Paired t test $t_{19} = -3.75$, $P = 0.001$, Figure 2.3). After TDR removal, the provisioning rates of the partners were significantly higher than those of the previously equipped birds (ANOVA: $F_{1, 39} = 14.36$, $P = 0.01$). There were no differences between males and females within each group (TDR-equipped birds: female = 1.98 ± 0.30 meals day $^{-1}$, male = 2.23 ± 0.55 meals day $^{-1}$; Student's t test: $t_{18} = 1.02$, $P = 0.32$; partners: female = 3.66 ± 0.41 meals day $^{-1}$, male = 3.57 ± 0.42 meals day $^{-1}$, Student's t test: $t_{18} = 0.78$, $P = 0.44$).

The pair-wise comparisons for the total provisioning rates of pairs with a TDR-equipped bird revealed no significant differences before and after TDR deployment (Paired *t* test: $t_{19} = 0.986$, $P = 0.336$) and before TDR deployment and after TDR removal (Paired *t* test: $t_{19} = -2.044$, $P = 0.055$, Figure 2.3). However, the provisioning of both parents was significantly lower after TDR deployment than after the TDR removal (Paired *t* test: $t_{19} = -3.421$, $P = 0.003$, Figure 2.3).

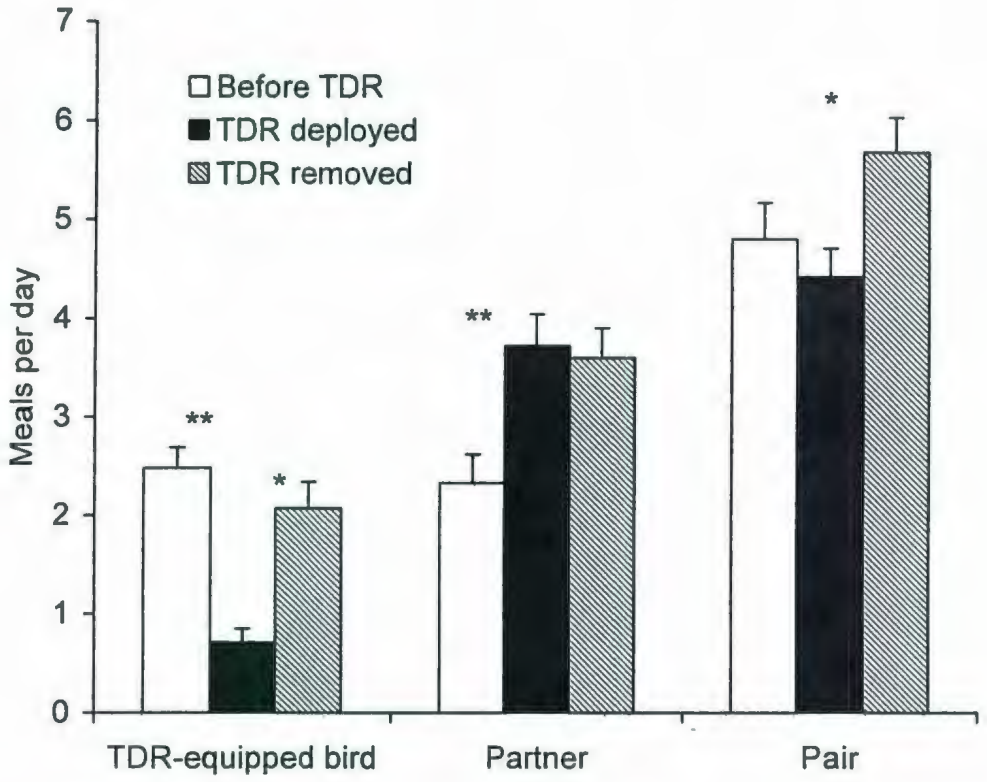


Figure 2.3 Provisioning rates (mean ± SE) of TDR-equipped birds and their partners ($N = 20$ pairs) before and after TDR deployment, and after TDR was removed. Pair represents the total provisioning of TDR-equipped birds and their partners. Asterix * denote statistical differences between groups (paired t tests: * $P \leq 0.003$; ** $P < 0.0001$).

To compare the total chick provisioning of control pairs and pairs with a TDR-equipped bird before and after TDR deployment and after TDR removal (TDR stage) I matched chick age with TDR stage to control for age effects in both pair groups. Before TDR deployment, chicks were up to 7 days old, during TDR deployment chicks were between 4 and 11 days old and after TDR removal chicks were between 12 and 15 days old. The total chick provisioning per pair was not affected by whether a member of a pair

was given a TDR (ANOVA: $F_{1, 133} = 3.758$, $P = 0.055$), but was significantly affected by TDR stage ($F_{2, 133} = 9.957$, $P = 0.0001$). There was no interactive effect of the factors on chick provisioning ($F_{2, 133} = 2.429$, $P = 0.092$; Figure 2.4). A post-hoc analysis revealed that pairs provided significantly less food before TDR deployment than after TDR deployment and TDR removal (Tukey HSD: $P < 0.05$). After TDRs were deployed, the pairs with a TDR-equipped bird provided significantly less food to their chicks than did control pairs (ANOVA: $F_{1, 62} = 10.988$, $P = 0.002$). However, there were no differences in the amount of food provided by the two types of pairs (control and TDR-equipped), when matched for chick age, before TDR deployment ($F_{1, 36} = 0.039$, $P = 0.845$) or after TDR removal ($F_{1, 35} = 0.520$, $P = 0.475$; Figure 2.4).

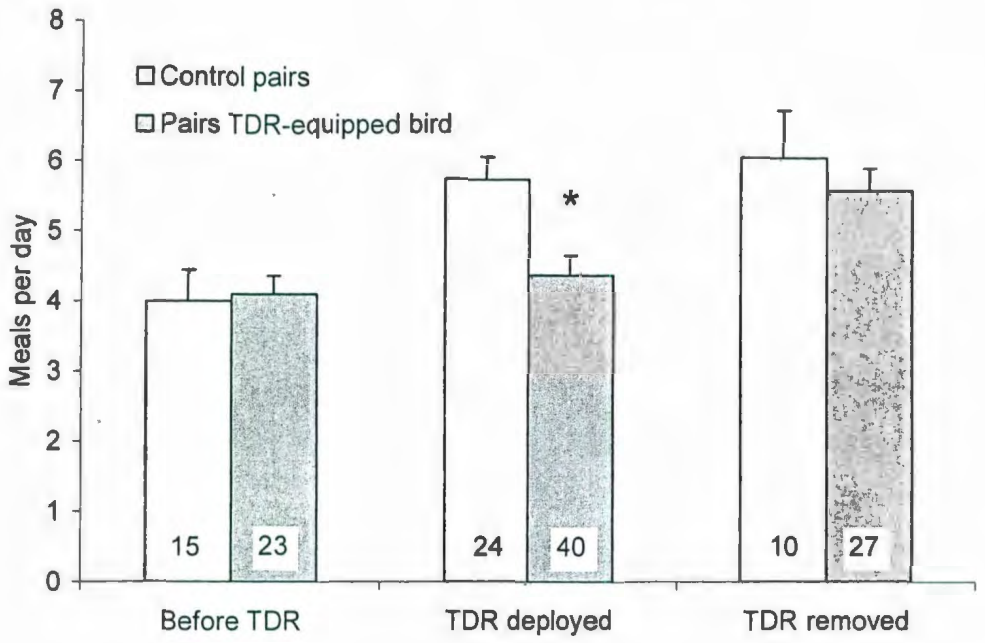


Figure 2.4 Total provisioning of control pairs and pairs with a TDR-equipped bird according to treatment stage (before TDR deployment, TDR deployed, and after TDR removal). Means are given ± SE. An asterix * denotes statistical difference between groups (ANOVA, $P = 0.002$).

2.4.3.2 *Offspring attendance*

The partners of TDR-equipped birds fully compensated for their mates' reduced offspring attendance (see above) of their mates, such the chicks were never observed to be left unattended. In order to confirm these results, and also to account for possible individual differences between control and TDR-equipped birds, I undertook paired t-test comparisons before and after TDR deployment. The TDR-equipped birds reduced the time spent brooding their chicks after TDRs were deployed (before: 12.39 ± 0.65 h day $^{-1}$, after: 10.05 ± 0.64 h day $^{-1}$; Paired *t* test: $t_{23} = 3.462$, $P = 0.002$), whereas their unfettered mates increased their time significantly (before: 11.67 ± 0.66 h day $^{-1}$, after: 14.04 ± 0.63 h day $^{-1}$; $t_{23} = -3.666$, $P = 0.001$). Both sexes of the instrumented birds spent significantly less time at the breeding site after TDRs deployment (Female: Paired *t* test: $t_{13} = 3.317$, $P = 0.037$, Male: Paired *t* test: $t_{9} = -2.676$, $P = 0.025$). For partners of TDR-equipped birds, both females (Paired *t* test: $t_{9} = -2.676$, $P = 0.025$) and males (Paired *t* test: $t_{13} = -2.332$, $P = 0.025$) increased their time brooding the chicks significantly after TDR deployment.

2.4.4 Fledging success

Of the 40 birds equipped with TDRs, three lost their chicks after deployment. One abandoned its breeding site after two days of breeding site attendance, another accidentally dislodged its chick during a fight with a neighbor and a third lost its chick

for unknown reasons several days after the TDR was removed. Nevertheless, fledging success did not differ significantly between TDR-equipped birds (0.92 fledglings year $^{-1}$, $N = 39$) and control birds (0.92 fledglings year $^{-1}$, $N = 12$, Student's t test: $t_{49} = 0.071$, $P = 0.994$). It was not possible to determine fledging success for one control and one TDR-equipped bird that were late breeders.

2.4.5 Reproductive costs

The rate of return to breed the following year was lower for TDR-equipped birds (83%, $N = 40$) than for control birds (96%, $N = 26$). The odds of return dropped significantly from 25:1 (TRD-equipped birds) to 4.74:1 (control) as expected (odds ratio = 0.181, Chi-Square test: $\chi^2_1 = 2.918$, $P = 0.044$ one-tailed). Of the TDR birds that did not breed, three were females and four were males. In contrast, the TDR-equipped birds' partners (88%, $N = 18$) returned to breed at a similar rate to control birds (Chi-Square test: $\chi^2_1 = 0.950$, $P = 0.329$). Reproductive success did not differ significantly between control birds (0.89 fledglings, $N = 26$) and those equipped with TDRs the previous year (0.88 fledglings, $N = 33$; ANOVA: $F_{1, 58} = 0.014$, $P = 0.996$). Overall breeding success did not differ between TDR-equipped females (0.81 fledglings, $N = 21$) and males (0.89 fledglings, $N = 19$; Student's t test: $t_{38} = 0.740$, $P = 0.464$).

A sub-sample of control pairs and pairs with a TDR-equipped bird (both members individually banded) were followed the next year to determine mate fidelity. Of the pairs that had a TDR-equipped member the previous year, one (2000: $N = 5$), four (2001: $N = 9$) and one (2002: $N = 5$) changed their mates the following year. All control pairs in 2000 ($N = 4$), 2001 ($N = 3$), and 2002 ($N = 4$) maintained their breeding site and mates the following year. Overall, a significantly higher proportion of pairs with a TDR-equipped birds member (32%, $N = 19$) bred with a different mate in comparison to control birds (0%, $N = 11$; Chi-Square test: $\chi^2_1 = 4.342$, $P = 0.037$). Of these pairs that divorced, previously TDR-equipped birds were not seen breeding except for one female that moved to a different breeding site. In contrast, most unencumbered partners (3 males and 2 females) stayed on the same breeding site with a different adult. Of these birds, two successfully fledged chicks, two lost their eggs/chicks and one bred very late in the season so breeding success could not be determined.

The second year after TDR deployment, fewer birds that had been equipped with TDRs (68 %, $N = 35$) were seen breeding at the colony in comparison to control birds (88%, $N = 26$; Chi-Square test: $\chi^2_1 = 3.34$, $P = 0.034$ one-tailed). A similar proportion of males (3/14) and females (9/21) previously equipped with TDRs did not breed the following year. Of these 12 birds, six of their partners were individually banded and five of these were seen breeding with a different adult. Whether the birds equipped with TDRs were not seen because they changed their mates at the beginning of the season, omitted reproduction, or died was unknown.

2.5 DISCUSSION

I was able to satisfy both initial objectives of this study on a long-lived seabird because I found clear negative effects of time-depth recorders on parental effort, thereby setting up the opportunity to examine compensatory parental behaviour experimentally using a handicapping approach.

2.5.1 Effect of time depth recorders on parental behaviour

Although my instruments were substantially less intrusive (3% of the body mass and 2% of cross-sectional body area) than the criteria (5%) used by most investigators for acceptable externally attached devices (Cochran 1980; Wilson *et al.* 1986) and smaller and lighter than those used in previous murre diving studies (Croll *et al.* 1992; Falk *et al.* 2000), I found that instrumented thick-billed murres suffered a reduction in body mass, offspring attendance, provisioning rates and frequency of foraging trips compared to non-equipped control birds. For equipped males only, increased foraging trip duration also occurred. Handling non-instrumented control birds similarly to the TDR-equipped birds eliminated the possibility that these effects were associated with stress due to manipulation.

Individual and inter-annual variation can also be excluded as factors that explain differences in foraging trip duration (Ballard *et al.* 2001) and provisioning rates of TDR-equipped birds. I found that foraging trips of equipped and control birds did not always end with chick feeding. In Cory's shearwaters (*Calonectris diomedea*), non-feeding visits were a regular occurrence when increments of chick weight were taken into account (Granadeiro *et al.* 1999). Thus, short or long foraging trips may in fact result in normal, reduced or no food delivery to chicks, so inferences about parental and foraging effort using only breeding site visitation (e.g. Jones *et al.* 2002a) and time spent at sea (e.g. Ballard *et al.* 2001) may lead to confusing conclusions. Additionally, the consistent findings with respect to provisioning rates using a longitudinal analysis before and after TDR deployment within a year and the cross-sectional analysis (control vs. equipped birds) support the idea that a device effect was the main cause of reduced parental effort of TDR-equipped birds.

In short, I believe the most likely explanation for my results is the physical effect of the device on murre flight (Obrecht *et al.* 1988) and underwater swimming performance (Bannash *et al.* 1994). The associated increase in energy costs experienced by TDR-equipped birds during foraging (Gessaman & Nagy 1988) would have caused a reduction in body condition, and an increase in maintenance effort with a consequent reduction in parental care.

Previous efforts attempting to measure the effect of instrumentation on the behaviour of individual animals may have used inadequate measures (e.g. Cairns *et al.* 1987; Croll *et al.* 1992; Benvenuti *et al.* 1998; Falk *et al.* 2000; Jones *et al.* 2002a). For example, I found that measures such as survival and success showed no difference between instrumented and non-instrumented birds, but parental behaviour was clearly affected. The tendency for partners to compensate seems to mask these effects on individual behaviour and total parental effort. Some studies that have tested the effect of TDRs in animal behaviour have found that individuals can compensate for the "extra workload" without disrupting their parental performance (e.g. seals: Boyd *et. al* 1991; Harcourt *et al.* 1995; seabirds: Weimerskirch *et al.* 1995; Schaffer *et al.* 2003; Kato *et al.* 2000). Others have shown that breeding individuals carrying data loggers had extended foraging trips (penguins: Croll *et al.* 1991; Watanuki *et al.* 1992; Hull 1997; Ropert-Coudert *et al.* 2000; Taylor *et al.* 2002) and reduced chick provisioning (alcids: Wanless *et al.* 1988; this study). Recent efforts to reduce drag of instrumented birds during swimming and flying have used new attachment methods. Implanted data loggers seem to reduce the effect of external attached devices in king penguin's foraging behaviour (Ropert-Coudert *et al.* 2000). However, they can affect the breeding success and increase mortality of murres and puffins (Meyers *et al.* 1998; Hatch *et al.* 2000). Ventral attachment of TDRs seems to reduce physiological stress in common murres, but affects their frequency of nest site visitation (Tremblay *et al.* 2003). The quantification of parental behaviour is a non-invasive method to infer gear effects on diving performance of free-ranging birds with external devices. Further research (i.e. using dummy TDRs) is

required to determine the optimal size, mass and shape of instruments so that behaviour is not affected and reliable activity data can be collected.

2.5.2 Compensatory behaviour and reproductive costs

According to models of biparental care (Houston & Davies 1985; McNamara *et al.* 1999), only a partial compensation by individuals for a reduced parental effort of their partners is expected in a stable evolutionary strategy. My results with respect to chick provisioning concur with these predictions and support other handicapping studies in birds (Wright & Cuthill 1989, 1990; Whittingham *et al.* 1994; Markman *et al.* 1995). I found that partners of encumbered murres increased their feeding rates above the average rates of control birds, so total amount of food delivered to chicks per day equaled that provided by both parents before TDR deployment. Even though this compensation was not enough in magnitude to equal the total provisioning rate of control pairs, it was sufficient for chicks to fledge at a similar rate to control birds.

In Antarctic petrels, handicapped birds also reduced their chick feeding frequency, however their non-manipulated partners did not compensate for this reduction, and chick loss was higher than for control birds (Saether *et al.* 1993). Foraging costs may be significant for this species, which has to travel long distances (400 km) during a prolonged chick-rearing period (45 days). I suggest that responses of seabird species to handicapping may be dependent on their life history strategies and individual energy

thresholds to different costs during reproduction (Jan-Ake 2002). In fact, handicapped thin-billed prions, *Pachyptila belcheri*, were able to feed their chicks at a similar rate to control birds at the expense of a reduction of their body mass (Weimerskirch *et al.* 1995). Within seabirds, thick-billed murres have the shortest chick-rearing period at the breeding site (15–20 days) of any species except murrelets (*Synthliboramphus;* Gaston & Jones 1998) and can deliver only one fish at a time. Thus, birds must commute between foraging areas and the breeding site several times per day (Gaston & Jones 1998). The reduction in frequency of foraging trips and body mass of TDR-equipped birds suggests chick provisioning is energetically costly. With only a single offspring at the breeding site, individuals face the prospect of zero reproductive success if they do not compensate for an indolent or disabled mate. A drastic reduction of chick provisioning may lead to a longer time at the breeding site for both parents, or cause poor chick development and likely increase chances of mortality at departure (Gilchrist & Gaston 1997). I found that the duration of the chick-rearing period by pairs with a TDR-equipped member did not differ from those of control pairs, which suggest maintenance of growth rates may be beneficial for both parents and offspring survival. Future research on other auk species that provision chicks at the nest site until they are full-sized (e.g. puffins) would help to better understand the mechanisms underlying compensatory behaviour.

After TDR removal, the previously equipped birds increased their feeding rates to values before TDR deployment. Their mates unexpectedly maintained their high provisioning rates, so the total amount equaled those of control pairs. After TDR removal, chicks were larger and received considerably more food than before TDR

deployment in control nests. Thus, the magnitude of the recovery of TDR-equipped birds might not have fully met the feeding demands of larger chicks. A complete recovery of the instrumented birds and the consequent reduction of their mates' feeding rates seems to occur later on, but this prediction requires further study.

Contrary to partial compensation in chick provisioning, I found that partners of TDR-equipped birds fully compensated for a temporary daily reduction of offspring attendance by increasing their time at the breeding site. Chicks were never observed unattended. As thick-billed murres breed in dense colonies where temporary abandonment is likely to yield chick mortality, full compensation is what would be expected based on recent models of biparental care (Jones *et al.* 2002b) that predict this when breeding success is an accelerating function of parental effort, (e.g., high nest site density and high predation levels). In yellow-legged gulls, *Larus cachinnans,* females did not compensate for a reduced incubation time of their males with testosterone implants (Alonso-Alvarez 2001). However, the fact that hatching success was not affected by a temporary abandonment of the eggs suggested compensatory behaviour was not crucial for chick survival.

Two surprising findings arise from the handicapping study. First, individuals were able to increase their parental effort above normal limits to cover their partner's deficiency when food availability was apparently normal. Second, the level of compensation to a reduced partner's effort (full or partial) was related to individual costs

of males and females towards different aspects of parental care and the consequent likelihood of breeding failure.

Parental roles and levels of energy allocation are not necessarily equal between males and females in species with biparental care (e.g. Hamer & Furness 1993; Gray & Hamer 2001). Therefore compensatory responses to reduced parental effort of impaired mates may also vary according to different parental roles between sexes (Sanz *et al.* 2000). Generally, parental behaviour of male and female murres in this study was similarly affected by the strain imposed by attached TDRs. Nevertheless, TDR-equipped males lost weight at a higher rate than TDR-equipped females. I also found overall that males, including control birds, spent more time at the breeding site and made longer foraging trips than females. These results suggest foraging strategies may differ between sexes in thick-billed murres as suggested by a previous study at Gannet islands on this subject (Jones *et al.* 2002a). However, chick provisioning did not differ between sexes in control pairs with chicks up to 11 days old. Both males and females responded similarly to the reduction in chick provisioning of their partners; and although control females spend less time with the chicks, TDR-equipped partners fully compensated for the absence of their encumbered partners at the breeding site. Compensatory behaviour seems not to be related to parental roles, but to reproductive values and costs of increased parental effort for males and females.

Parents that provide biparental care have common and conflicting interests, and in theory, males and females are expected to compete to provide the minimum parental

effort to ensure their individual fitness (Williams 1966). My results are consistent with these predictions of dynamic game models of parental effort (Houston & Davies 1985; McNamara *et al.* 1999), and further support the behavioural flexibility and cooperation of truly monogamous long-lived species. The compensatory responses of males and females to reduced partner effort are likely the result of their obligated biparental care and life history strategies.

Several authors have suggested that long-term relationships in monogamous species can help to synchronize parental activities, reduce energy allocation in mating and therefore increase lifetime reproductive success (Cooke *et al.* 1981; Fowler 1995; see Black 1996; Black 2001). In this context, it would be advantageous for individuals of long-lived species to maintain the condition of their partners and ensure their survival, so compensation to reduced partner's effort would be more likely to occur. Although I found that all thick-billed murres compensated for the reduction of parental effort of their handicapped partners, I also found that these birds tended to change their mates in each of the three study years, while control pairs showed total mate and site fidelity. Divorce in monogamous birds is more likely to occur if there is a reproductive failure or if one member of a pair shows poor quality as a parent (reviewed in Choudhury 1995; see Black 1996). Common murres pairs (12/30) with low reproductive success divorced the following season, and those individual that change mates have higher reproductive success (Moody *et al.* 2005). This may explain my results in part because although breeding success of pairs with a handicapped bird was not affected, there was a clear reduction on parental performance by the TDR-equipped mate. Less experienced or

young birds are expected to be more likely to be divorced if mates show poor parental performance in thick-billed murres (Gaston & Hipfner 2000) and other birds (Rowley 1983; Choudhury 1995). Thus, young birds (or others with recently established pair bonds) that are forced to compensate may subsequently divorce their "poor quality" mates to reduce costs in future breeding seasons. Several authors have suggested that divorce should be seen as a tactic by an individual to increase fitness (see review Choudhury 1995). The lack of known-age birds and fitness information for my study population precludes us from making conclusions about these predictions. Even though not mutually exclusive another explanation for the higher rates of divorce of pairs with a TDR-equipped member is the mortality of their mates. I found that previously TDR-equipped birds returned to breed less often than their partners and control birds, which suggest handicapping, might have affected their survival. However, it is also possible that TDR-equipped birds left the colony because they failed to re-mate at the beginning of the season, when I was not doing observations.

In summary, individual thick-billed murres' body condition and behaviour was affected by carrying TDR data loggers. Both males and females were able to fully or partially compensate for a reduction of parental effort by their handicapped partners to ensure breeding success. Although, compensatory behaviour seems to be a necessary response for breeding success in this single brooded species, it might also affect the stability of pair bonds of some individuals.

2.6 ACKNOWLEDGMENTS

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CHAPTER 3: SEX DIFFERENCES IN DIVING BEHAVIOUR OF THICK-BILLED MURRES AND RAZORBILLS AT THE GANNET ISLANDS, LABRADOR

3.1 ABSTRACT

Empirical evidence suggests sympatric seabird species partition the resources of their environment. Within species, the reasons behind sex differences in foraging behaviour remain unclear. Sympatric thick-billed murres (*Uria lomvia*) and razorbills (*Alca torda*) have distinct foraging strategies and their sexes differ similarly in parental roles. I tested whether males and females in these species at Gannet Islands, Labrador differed in their diving behaviour and prey choice during the chick-rearing period. Murre males dived deeper (34.5 m ± 21.32 SD vs. 19.7 m ± 17.9 SD) and longer (120 ± 44.1 SD s vs. 88.8 s ± 44.3 SD) than females, which appear to be associated to the time of day they foraged. Males dived mostly during mid-day to early afternoon whereas females dived after dawn and before dusk. In razorbills, although there were no clear sex differences in the main dive parameters and foraging times, female razorbills tend to dive more often at twilight and to shallower depths (<10 m) than males (10-27 m). The tendency for shallow diving by females of both species may explain their shorter bouts despite the equal number of

dives per bout and per day between sexes. I also found sex differences in dive profiles and prey in both species. Female dives were mostly shallower W-shaped dives, probably for capturing crustaceans at twilight. In contrast, males performed mostly deeper U-shaped dives for capturing mid-water species (e.g., capelin *Mallotus villosus*). Razorbill dives for capturing shallow schooling species (e.g., sand lance *Ammodytes sp.*) were V-shaped. Altogether, my results suggest that two sympatric auks had relatively similar inter-sexual segregation in water depth, time of day, and prey during reproduction. Females tend to dive in shallower waters than males, which reflects in their dive shape profiles and prey species. Sex differences in nest attendance, driven by differences in parental roles, seem to explain these findings.

3.2 INTRODUCTION

According to niche theory, species coexisting at equilibrium must partition the resources of their environment until inter-specific competition becomes less significant than intra-specific competition (Hutchinson 1978; Ricklefs 1990). In seabirds, empirical evidence indicates partitioning of food resources occurs in related sympatric species by habitat, prey choice (McGinnis & Emslie 2001; Day *et al.* 2003) and foraging times (Lance & Thompson 2005). Other studies have shown that sexes can also differ in their foraging niches, which may reduce intra-specific competition for food resources (Casaux &

Barrera-Oro 2006; Breed *et al.* 2007). Sex differences in foraging behaviour in some marine mammals (seals: e.g., Beck *et al.* 2003; Page & Goldsworthy 2005; killer whales: Baird *et al.* 2005) and seabirds (penguins: Bethge *et al.* 1997; Clarke *et al.* 1998; Bearhop *et al.* 2006; cormorants: Kato *et al.* 2000; Ishikawa & Watanuki 2002; Cook *et al.* 2007; and auks: Jones *et al.* 2002) is explained by sexual size dimorphism (i.e. body mass and bill size, review Halsey *et al.* 2006). The larger sex is able to forage over greater distances and to deeper sections of the water column (Weimerskirch *et al.* 1997; Kato *et al.* 2000; Ishikawa & Watanuki 2002). They may also forage on larger prey (Cook *et al.* 2007). Sex differences in foraging behaviour have also been found in several monomorphic seabird species (Bethge *et al.* 1997; Lewis *et al.* 2000; Jones *et al.* 2002; Peck & Congdon 2006), which suggests other factors can explain the differences found between males and females.

Thick-billed murres (*Uria lomvia*) and razorbills (*Alca torda*) are generally monomorphic with slightly differences in some body measurements (Gaston & Jones 1998). These alcids are wing-propelled divers with distinct foraging strategies; thick-billed murres are single loaders and mid-deep water divers while razorbills are multiple-loaders and shallow-mid water divers (review by Gaston and Jones 1998; Gaston and Hipfner 2000; Hipfner and Chapdelaine 2002). Although thick-billed murres' diving behaviour has been extensively studied across their geographic range (Croll *et al.* 1992; Falk *et al.* 2000; Melhum *et al.* 2001, Watanuki *et al.* 2001; Benvenutti *et al.* 2002; Jones *et al.* 2002; Mori *et al.* 2002; Watanuki *et al.* 2006) only one study has examined possible

differences between the sexes (Jones *et al.* 2002). Razorbills' diving behaviour has been studied much less and no studies have investigated possible sex differences (Benvenutti *et al.* 2001, Dall' Antonia *et al.* 2001, Watanuki *et al.* 2006).

Regardless of the species differences in foraging tactics, murre and razorbill males and females share similar partitioning in parental roles — biparental care is provided at the breeding site for two weeks and uni-paternal care at sea for 3-4 weeks (Gaston and Jones 1998). At the Gannet Islands, Labrador, females are the main meal providers while males are mostly involved in brooding and chick defence (Paredes *et al.* 2006). The intriguing question is whether these patterns in parental behaviour determine the foraging and diving behaviour of males and females. In other monomorphic seabirds, the sex with the shorter foraging trip also feeds the chick more frequently (Gray and Hamer 2001; Peck and Congdon 2006; but see Lewis *et al.* 2002). At the Gannet Islands, murres and razorbills followed the same pattern between the sexes (Paredes *et al.* 2006). The fact that sex differences only occurred during trips with meal delivery suggested that foraging tactics of males and females were motivated by their parental duties. Whether sex differences in trip duration were due to differential diving activity or distance to feeding areas was unknown. Sexes could potentially forage at different times because of differences in breeding site attendance patterns (i.e. thick-billed murres: Woo in Gaston and Hipfner 2001; Jones et al. 2002; Paredes *et al.* 2006). In Crested Auklets (*Aethia cristatella*), males brood at night and dive by day, and they seem to be better suited to breeding site defence and chick guarding than females (Fraser *et al.* 2002). The male-

biased capability in defending the chick, because of larger bill dimensions and more aggressive behaviour (Chapter 5), is one of the proposed explanations for partitioning of parental roles in murres and razorbills (Paredes *et al.* 2006). Thus, it is possible that foraging schedules were driven by the need of males to be at the breeding site at times when the chick is potentially in most danger. If this were true, we expect males in both species to show foraging schedules that correlate with their parental behaviour. Consequently, they could potentially forage under different at-sea environmental conditions than females (i.e. light levels or prey availability), and therefore affect their dive depth and prey taken (Wilson *et al.* 1993; Jones *et al.* 2002) differently. Physical (water depth) and ecological constraints (prey species) play major roles in the frequencies of dive types and other dive parameters in a multi-species comparison of seabirds and pinnipeds (Schreer *et al.* 2001).

Functional classification of dives based on dive shape (i.e., time-depth profile) has been done for several species of air-breathing animals (Kooyman *et al.* 1992; Schreer and Testa 1996; Schreer *et al.* 2001). U- and V-shaped dives are the most frequent types observed in thick-billed murres (Croll *et al.* 1992; Elliot *et al.* 2008) and razorbills (Benvenuti et al. 2001; Dall'Antonia et al. 2001; Watanuki et al. 2006) respectively, however whether sex differences occur is unknown. Using stomach-temperature recorders, some studies have been able to confirm associations between dive shape and feeding (Thompson et al. 1991; Wilson *et al.* 1992a; Lesage et al. 1999). Thick-billed murres usually perform direct flights to the colony for chick delivery (Benvenuti et al.

2001). This distinctive behaviour has allowed for associations between dive shapes and specific prey species (Elliot et al. 2008). Others diving studies in northern gannets (*Morus bassanus* L., 1758; Garthe et al. 2000), and king penguins (*Aptenodytes patagonicus* Miller, 1778; Pütz and Cherel 2005) have also reported relationships between prey species and dive profiles. Sex differences in prey delivered to chicks have been reported for razorbills at Skommer Island (Wagner 1997), which may reveal differences in dive profiles as well. Thus, the analysis of dive profiles in relation to prey and daytime may be useful for understanding the mechanisms behind sex differences in diving behaviour.

The aim of this study was to investigate whether sexes of two sympatric sister-species, thick-billed murres and razorbills, differ in their foraging behaviour and prey captured; and whether these differences mirrored their parental roles. I specifically studied whether sexes differed in dive parameters, frequency of dives and dive bouts, dive type, and prey species for chick provisioning. Body mass and parental behaviour of a group of non-instrumented murres was investigated simultaneously to control for possible effects of attached gear on diving behaviour (Paredes *et al.* 2005).

3.3 METHODS

I conducted fieldwork during August 2000–2003 at one of the six Gannet islands (GC4) located on the low Arctic coast of Labrador, Canada (53°56′ N, 56°32′ W).

A mixed colony of about 150 pairs of thick-billed murres (murres from now on) and 45 pairs of razorbills were studied through the chick-rearing period. A total of 40 thick-billed murres and 18 razorbills were captured for deploying time-depth recorders (TDRs). Fifteen additional razorbills were captured, as part of another ongoing study, for sex determination. Only one member of a pair was captured for TDR deployment while the other was brooding, so the chick (1-11 days old) was never left unattended. Murres were captured with a noose of nylon monofilament (1.5 mm diameter) on the end of a 4-m graphite pole. Razorbills were captured with a small weighted noose-carpet attached to one end of 20 m of nylon monofilament line (1.5 mm diameter) and with the other end attached to 3-m wooden pole. The noose-carpet was positioned on cliff ledges, so razorbills were captured by the leg as they approached or departed their breeding site.

Two types of TDRs were deployed on murres - MK7 (Wildlife Computers, 25 g, 3 % of body mass, flat shape with pointed end) and LTD_100s (Lotek, 16 g, 2 % of body mass, cylindrical shape with rounded end). Both TDRs are similar in size (5–8 cm × 1–2 cm × 1–2 cm), and in cross-sectional area (1.7–1.9 cm^2, 1.2–1.3 % of the body area). I deployed LTD_100 units on razorbills. TDRs were attached onto the back of feathers using three strips of black TESA® tape, cable ties and drops of cyanoacrylate glue ("hot

stuff'®) under both ends of the device. Handling time from capture to release totalled between 5–8 minutes. TDRs were programmed to sample depth every 5 s and depth resolution was 0.5 m. I recovered TDRs several days after deployment (murres: 1– 4 days, razorbills: 2–7 days). Blood samples (0.5 ml) were taken from the tarsus vein and stored in vials with 95% ethanol for use in determining the bird's sex by DNA analysis (Fridolfsson & Ellegren 1999).

I performed daily observations of feeding of marked murres (15 pairs) and razorbills (31 pairs), including the instrumented birds; during most of the chick-rearing period. The observations were undertaken from a blind, using a spotting scope (20–60×, 60 mm) and binoculars (10×, 50 mm), from dawn to dusk (0400 h – 2200 h). Prey delivered to chicks was recorded at the species level when possible. I identified individual birds by temporary marks of picric acid (yellow) or fluorescent paint (green, pink and orange) delivered using a small container of the marking liquid attached to the tip of a 4 m graphite pole. This method allowed marking the birds from above without capturing them or disturbing the colony. The markings and key life-history information were recorded on ID cards for quick reference. One member of each pair was captured at the end of the chick-rearing period for permanent banding (a stainless steel and a colour leg band) and sex determination. The sexing analysis was done after the season was finished so the observers were blind to the sex of birds during behavioural data collection.

Data of ambient light intensity or total illumination (solar + lunar illumination) were inferred for the colony position using astronomical ephemeris (Eran Ofek: http://wise-obs.tau.ac.il/~eran/). These calculations do not account for cloud coverage. Based on these records, I determined that twilight periods occurred around dawn from 03:30 to 05:30 and around dusk from 20:00 to 22:00.

3.3.1 Data and statistical analysis

Dive data were analyzed using the dive analysis program from IKNOS toolbox (Y. Tremblay, unpublished) developed with MATLAB software (The MathWorks, Natick, Massachusetts). The program was setup to analyze all dives equal or exceeding 3 m depth (6 times depth resolution), and 15 seconds duration (3 times sampling interval). Dive parameters were calculated for each dive, following Tremblay and Cherel (2003). I determined maximum depth (depth), duration, bottom time (the amount of time between 75% and 100% of the maximum depth reached), and descent and ascent rates for individual dives. I calculated diving efficiency, the proportion of the bottom time over a complete dive cycle (dive duration + PDI, Ydenberg & Clark 1989). Because 95% of dives had a post-dive interval < 2 times their duration, this threshold was chosen as a bout ending criterion (Tremblay & Cherel 2003). Dive profiles were classified visually in five dive shape categories: V-, U-, square-, W-, and asymmetrical.

Of the 40 TDRs deployed on murres, 30 obtained data, seven had anomalous data and three fell off the birds before re-capture. I was unable to compare data between the sexes from both types of TDRs, ((MK7: 11 males and 15 females and Lotek: 3 males and 1 female), directly because only one female murre had a Lotek since I did not know the sex of birds at the time of deployment. Nevertheless, because most of the birds had MK7 units (26 of 30) I compared the dive records of them against those of both TDRs together (MK7+Lotek). In this way, I indirectly accounted for possible effect of type of TDR, and if the results were not affected by pooling the data I assumed this would allow us to include Lotek data for the analysis. Of the 18 TDRs deployed on razorbills (all Lotek), 9 obtained data recordings (6 females and 3 males), one had no data (female), and eight were never recovered.

A total of 4,716 dives and 1,668 dives were recorded from murres and razorbills respectively. I only used a total of dives performed during entire days (murres: females = 1,721 dives, males = 1,927 dives; razorbills: females = 1,082 dives, males = 473 dives) to be able to investigate time of day effects in diving behaviour.

Maximum depth reached during a dive affects other diving parameters in other species (Wilson *et al.* 1997; Tremblay & Cherel 2000). The analysis of other dive parameters can show whether sexes differ in their behaviour at the same water depths, which can indicate or not differences feeding tactics. When there were differences in depth between the sexes, I compared the standard deviates of dive parameters to provide an independent analysis of depth. Standard deviates [(value-mean)/SD] were calculated for all the dives belonging to every bin depth of 2 meters (Sokal & Rohlf 1998).

I used mixed factor models for the analysis of bouts, dive parameters and dive shapes. The fixed factor was sex, and individual was used as the random factor. In this way, we were able to include the effect of individual variation in the model. Statistical analysis was carried out using SPSS version 11.5. If residuals were not normally distributed, we transformed the dependent variable using log or square-root transformation as appropriate before the analysis and presented coefficient of variation (CV) instead of standard deviation (SD). We report 95% confidence intervals instead of estimates of statistical power to address the question of type II error (Hoenig and Heisey 2001). Chi-Square tests with Yates's correction were used to compare proportions. Relationships between parameters were analyzed using Pearson correlations. Means were expressed ± SD of the mean.

3.4 RESULTS

3.4.1 Non-effect of TDR type

The mean depth of individual dives was not affected by TDR type (MK7: 25.9 ± 20.8 m, both TDRs: 27.5 ± 21.1 m; mixed-factor model: $F_{1,53} = 0.053$, $P = 0.818$), but significantly affected by sex ($F_{1,28.21} = 19.21$, $P = 0.0005$). On average, male murres

(33.6 ± 21.4 m) dove 59% as deep as females (19.8 ± 18.0 m). Lack of significant effect of TDR type on the main factor allowed us to compare males and females in my analysis.

TDR effect on body mass

No sex differences were found in initial body mass in razorbills (female: 701 ± 51.8 g, N = 14, male: 711 ± 38.5 g, N = 19, Student t-test: $t_{[1,31]} = -0.651$, $P = 0.52$). On average, razorbills, regardless of sex (females: 16.4 ± 5.3 g /d, males: 13.7 ± 3.5 g/d, Student t-test: $t_{[1,6]} = 1.040$, $P = 0.338$) with TDRs lost 15.0 ± 4.8 g/ d during the deployment period. Male murres had higher initial body mass and lost weight at higher daily rates than females (Paredes *et al.* 2005).

3.4.2 Thick-billed murre diving behaviour

Murres at Gannet Islands showed a difference between the sexes in the time of day foraging occurred (Fig. 3.1). Most dives of female were between late afternoon and sunset (18:00–21:00, 70%, N = 1,721) and between early morning and after sunrise (03:30 – 06:00, 11 %), while most dives of males occurred during late morning to early afternoon (08:00 –19:00, 67 %, n = 1 927, Fig. 3.1). For twilight periods, females performed more dives near dusk (20:00 – 22:00 h, 56%) than dawn (03:30 – 05:30 h, 10%), while males performed only 7–9 % of their dives during these periods. Only 3% (

$N = 125$) of dives were recorded during darkness (22:00 – 03:00 h). These dives were shallow (< 10 m) and performed mostly by females (68%). Dive depth was positively correlated with inferred solar illumination, however some deep diving (up to 102 m) was also performed at times (05:00 – 07:00 h) when total illumination was low (Fig. 3.2).

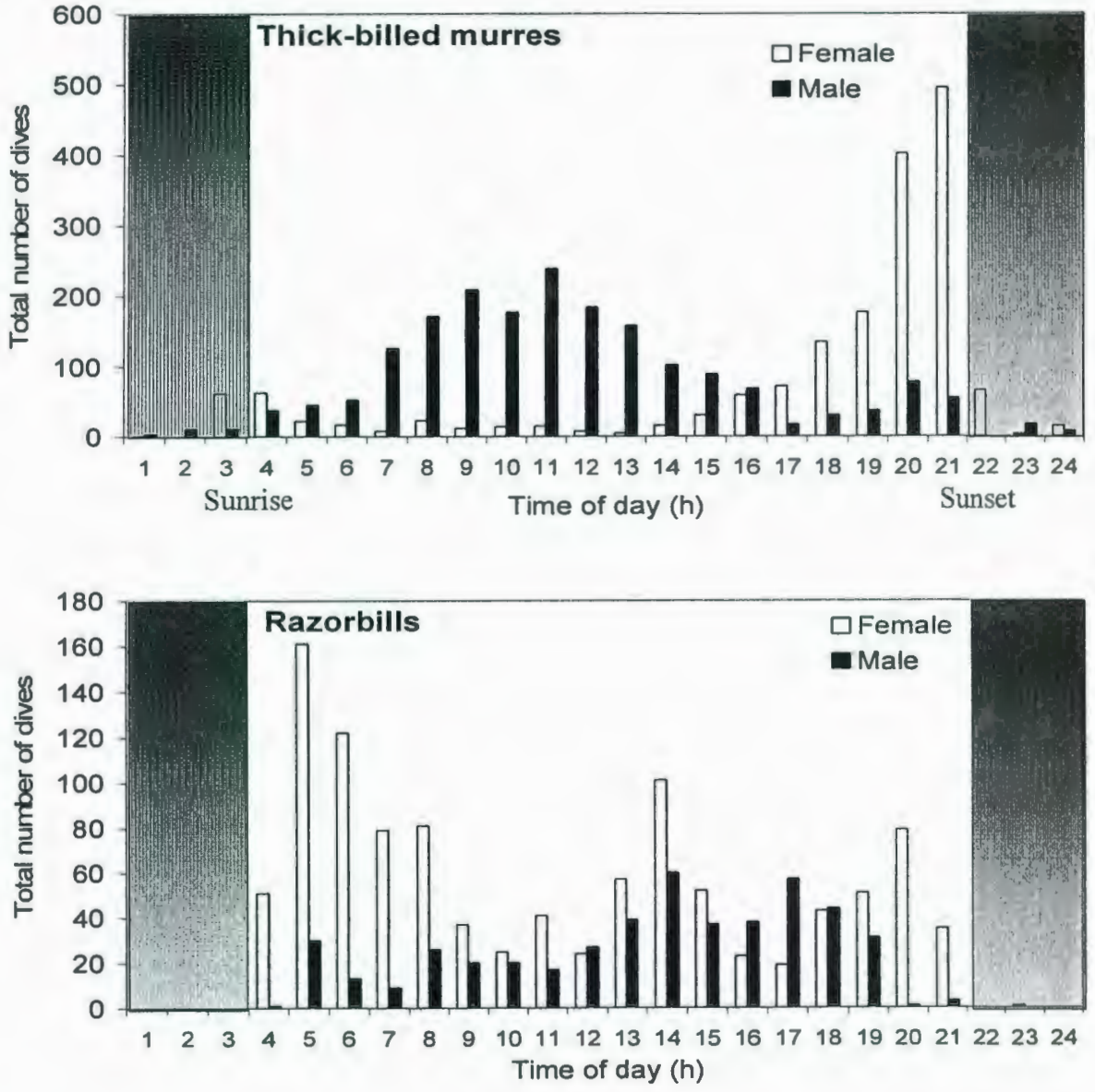
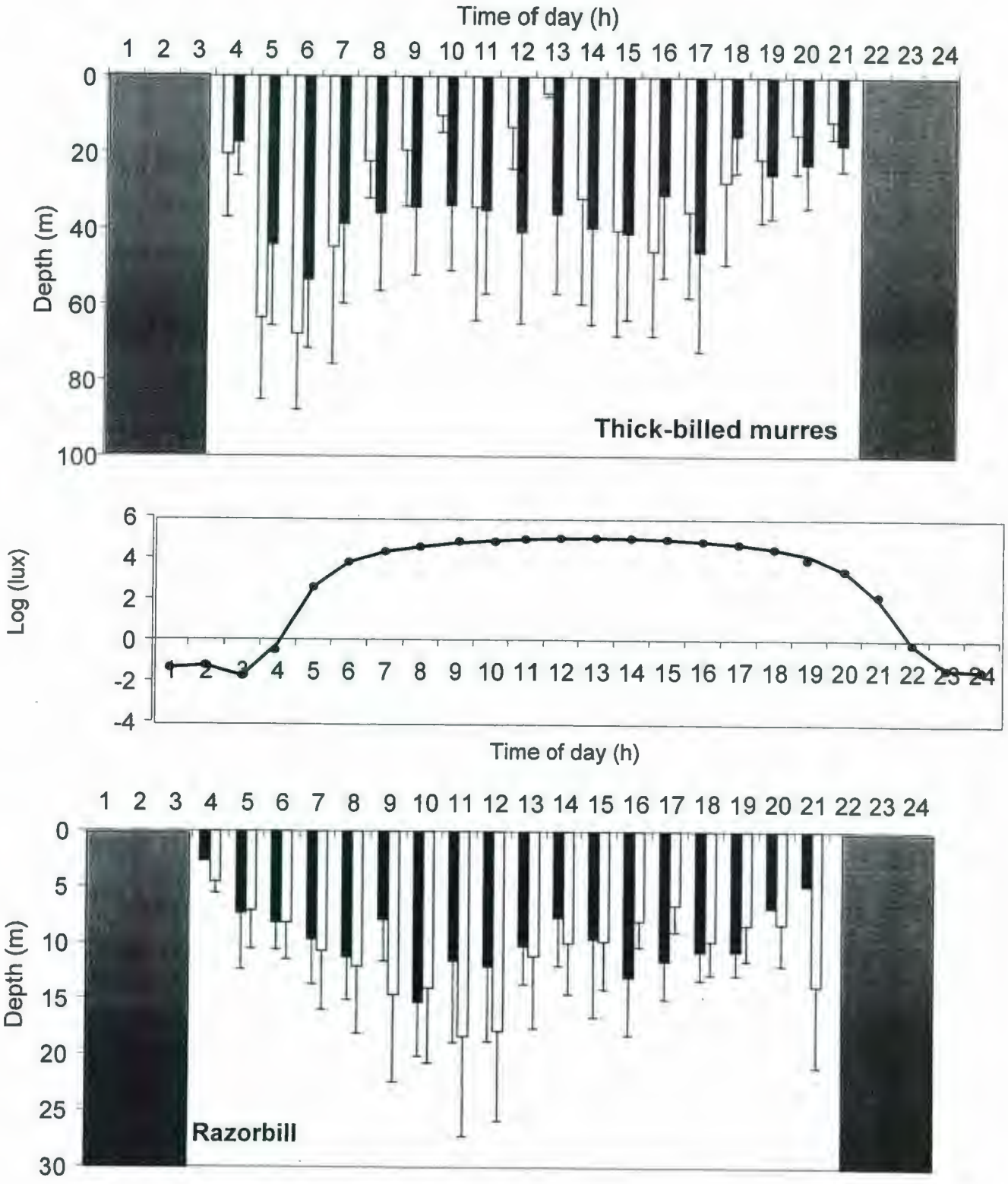


Figure 3.1 Number of total dives according to time of day of male and female thick-billed murres (males: $N = 14$; 1,927 dives; females: $N = 16$; 1,721 dives) and razorbills (males: $N = 3$; 473 dives, females: $N = 6$; 1,082 dives) at Gannet Islands, Labrador. Dark rectangules represent the darkness periods (10:00-03:00 h); night diving was infrequent or absent in murres and razorbills respecttively.

The depth of murres' dives was strongly related to the time of day (mixed- factor model: $F_{[23, 3\,574]} = 41.54$, $P < 0.0001$). However, male and female dive depths were affected differently by time of day (sex * time: $F_{[21, 3\,574]} = 9.88$, $P < 0.0005$). The deepest dives of females occurred early in the morning (05:00 –06:00 h, Post-hoc Tukey HSD test, $P < 0.0001$), and to a lesser degree early in the afternoon (15:00 – 17:00 h, Post-hoc Tukey HSD test, $P < 0.002$, Fig. 3.2). Males' deep diving also occurred early in the morning (05:00 – 07:00 h) but they occurred during mid-day and early afternoon as well (12:00 – 17:00 h, Post-hoc Tukey HSD tests, $P < 0.01$). The dives of both males and females were significantly shallower immediately after sunrise (03:00 – 04:00 h) and before sunset (20:00 – 23:00 h, Post-hoc Tukey HSD test: $P < 0.001$, Fig. 3.2).

Figure 3.2 Variation of dive depth of male (black bars) and female (white bars) thick-billed murres (males: $N = 14$, 1, 926 dives; females: $N = 16$, 1,721 dives) and razorbills (males: $N = 3$, 473 dives, females: $N = 6$, 1,082 dives) according to time of day (means ± SD) and total illumination (solar and moon illumination) at Gannet Islands. Statistical differences were found in the interaction term sex * time of day in both species (mixed- linear models: $P < 0.0005$).


Time of day (h)
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
Depth (m)
0 20 40 60 80 100
Thick-billed murres
Log (lux)
6 4 2 0 -2 -4
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
Time of day (h)
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
Depth (m)
0 5 10 15 20 25 30
Razorbill

Most dives by females occurred at shallower depths (73%, up to 19 m), and most dives by males (67%) occurred deeper in the water column (20–90 m, Fig. 3.3). There were significant differences in the proportion of dive shape groups between males and females ($\chi^2_{[4]} = 385.46$, $P < 0.0005$). On average, males dived significantly deeper (mixed-factor model: $F_{[1,28]} = 20.015$, $P < 0.0001$) and longer (mixed-factor model: $F_{[1,28]} = 16.55$, $P < 0.0005$) than females (Table 3.2). Females ($N = 1,721$) had significantly more W-shaped dives than males ($N = 1,927$), and males had more U-shaped dives than females ($\chi^2 = 370.77$, $P < 0.0005$, Table 3.1). We did not find sex differences among the other three groups of dive shapes, V-shaped, square-shaped, and other asymmetrical shapes of males (3%) and females (3%; $\chi^2 = 4.908$, $P = 0.086$, Table 3.1). On average W-shaped dives ($N = 2,133$) were significantly shallower than U-shaped dives ($N = 1,144$; mixed-factor model: $F_{[1, 68.55]} = 89.84$, $P < 0.0005$, Table 3.3). Females performed most W-shaped dives (70%) immediately before sunset (20:00 – 22:00 h), and most U-shaped dives during late afternoon onwards (67%, 15:00 – 20:00 h) and early morning (16%, 04:00 – 06:00; Fig. 3.6). In contrast, W-shaped and U-shaped dives of males were distributed in a similar manner according to hour of the day (05:00 – 16:00 h; Fig. 3.6). During nighttime (21:30 – 3:00 h) both sexes performed only W-shaped dives. These differences in the timing of diving between sexes correlated with differences in the parameters of dives of different shapes. W-shaped dives of males were significantly deeper (mixed-factor model: $F_{[1, 31]} = 15.648$, $P < 0.0005$) and longer ($F_{[1, 31]} = 8.781$, $P = 0.006$) than those of females. Likewise, W-shaped dives of males had longer bottom time ($F_{[1, 31]} = 13.19$, $P = 0.001$), faster ascent rate ($F_{[1, 31]} = 13.37$, $P =$

0.001) and longer post-dive interval ($F_{[1, 31]} = 9.57$, $P = 0.004$) than those of females (Table 3.4). No sex differences were found in descent rate and dive efficiency of W-shaped dives ($P > 0.05$; Table 2). We did not find differences in any diving parameters of U-shaped dives between males and females (mixed-factor models: $P > 0.05$; Table 3.4).

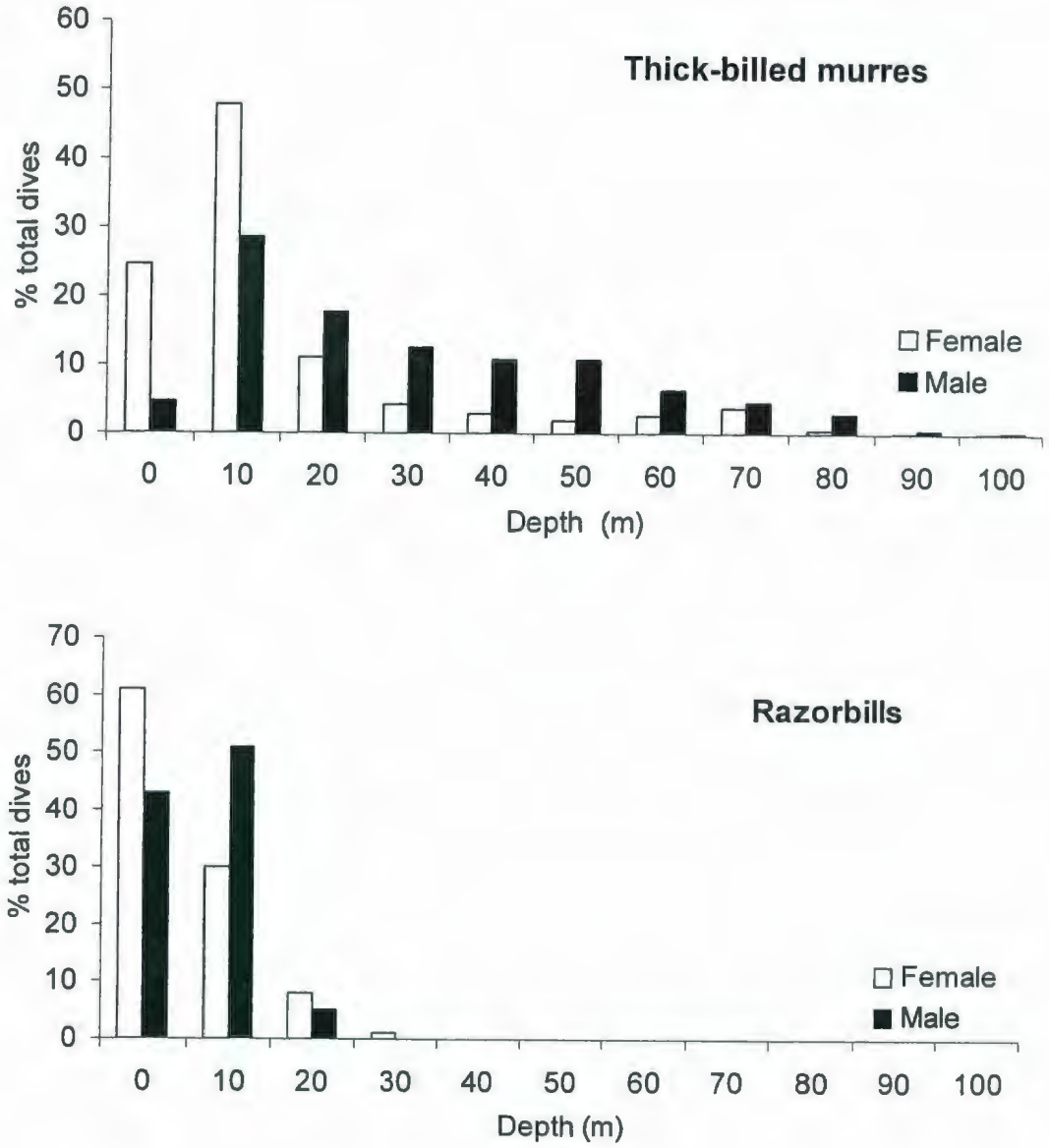


Figure 3.3 Frequency of dives of male and female thick-billed murre (males: $N = 14$, 1, 926 dives; females: $N = 16$; 1,721 dives) and razorbills (males: $N = 3$; 473 dives, females: $N = 6$; 1,082 dives) at 10 m-depth interval.

Table 3.1 Frequencies of the main type of dives of thick-billed murres (males: 1, 927 dives, females: 1,721 dives) and razorbills (males: 473 dives; females: 1,082 dives) at Gannet Islands, Labrador. Asterix (*) denote statistical significance (Chi-square tests: $P < 0.0005$).

Razorbill		Dive Shape	Thick-billed murres	
Female	Male		Female	Male
6%	21% *		17%	45% *
38%	18% *		75%	44% *
1%	6% *		4%	6%
43%	40%		2%	3%

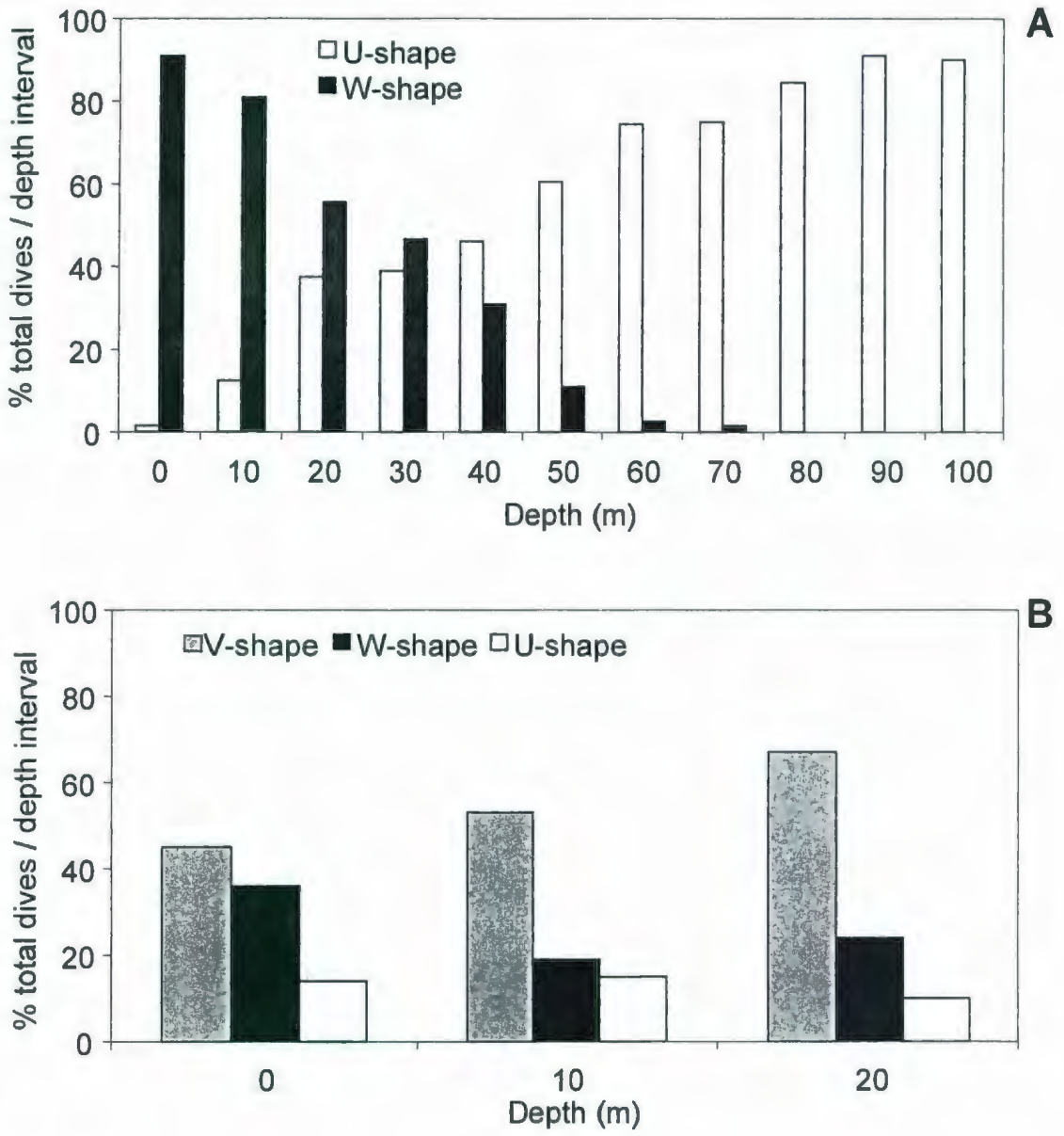


Figure 3.4 Frequency of the main dive shape categories according to depth for thick-billed murres (U- and W-shaped;) and razorbills (V- U- and W-shaped). Proportions of dive shapes are based on the total number of dives per 10 m-depth category.

Dive duration was positively correlated with depth (duration = 14.9 m/ s depth + 0.4 s, r^2 = 0.89, P = 0.001; Fig. 3.5) and post-dive interval (PDI) in murres (PDI = 24.4 s + 0.8 duration, r^2 = 0.65, $P < 0.001$). Males dive deeper and had longer bottom time, PDI, dive cycle and faster ascent and descent rates than females (mixed-factor models: $P < 0.007$; Table 3.2). Despite differences in dive depth, sexes did not differ in diving efficiency (Table 3.2). The differences in other dive parameters bewteen the sexes disappeared when depth was controlled for, except for PDI. Female murres had significantly longer post-dive intervals than males independently of the depth of the preceding dive (Table 3.2).

Males had longer bouts than females (mixed-factor model: $F_{[1, 28]} = 7.66$, $P = 0.009$); but they did not differ in the daily number of dives (mixed-factor model: $F_{[1,28]} = 0.69$, $P = 0.420$), and bouts (mixed-factor model: $F_{[1,28]} = 0.150$, $P = 0.701$). Sexes did not differ in the number of dives per bout per day (mixed-factor model: $F_{[1, 28]} = 0.400$, $P = 0.532$; Table 3.2).

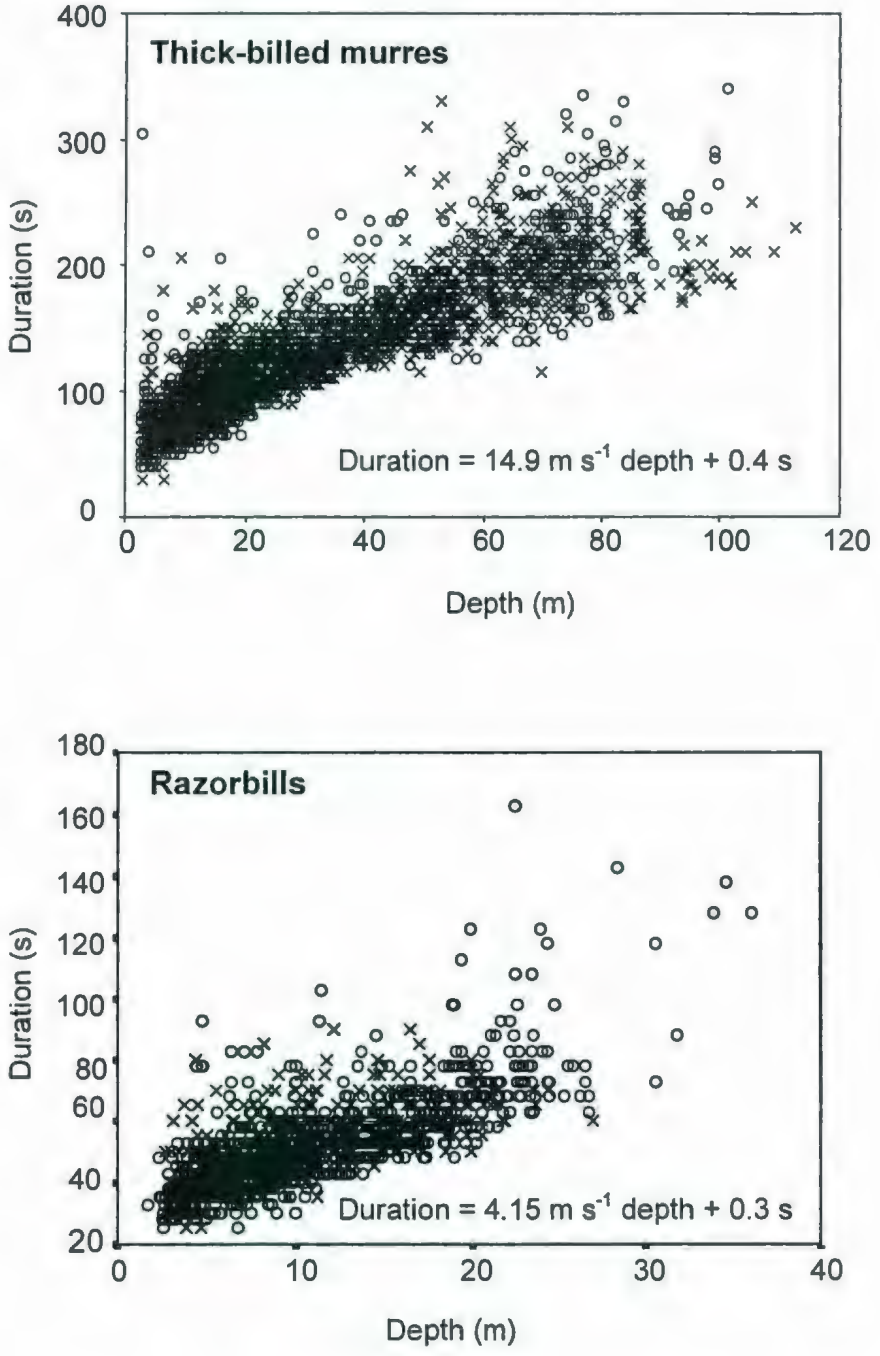


Figure 3.5 Relationship between dive depth and duration in thick-billed murres and razorbills (female = O and male = X) at Gannet Islands, Labrador

Table 3.2 Dive parameters of male and female thick-billed murres (F = 16, M = 14) and razorbills (F = 6, M = 3) at Gannet Islands, Labrador. The total number of dives is shown in parenthesis. Asterix (*) denotes statistical significance between the sexes: ** $P < 0.0001$, $P < 0.007$.

	Thick-billed murres				Razorbills			
	Female (N = 1,721)		Male (N =1,927)		Female (N = 1,082)		Male (N = 483)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Max. dive Depth (m)	19.69	17.89	34.52**	21.32	9.94	5.78	10.4	4.9
Dive Duration (s)	88.79	44.33	120.05**	44.11	48.32	14.73	52.1	11.7
Bottom time (s)	35.79	17.75	47.05**	17.23	19.15	5.22	21.8	5.94
Ascend rate (m s^{-1})	0.594	0.239	0.823*	0.289	0.608	0.250	0.65	0.26
Descend rate (m s^{-1})	0.755	0.269	0.882*	0.259	0.538	0.180	0.54	0.17
Post-dive interval [a] (s)	43.62	50.29	66.34*	50.85	25.12	22.75	25.1	23.1
Dive cycle [a] (s)	127.84	79.85	181.9*	82.09	74.89	29.18	78.1	16.4
Diving efficiency [a] (s)	0.332	0.125	0.311	0.122	0.320	0.091	0.33	0.10
N dives per day	53.70	25.19	49.41	29.86	54.10	26.37	43.00	34.65
N bouts per day	11.00	4.69	10.38	4.62	17.25	8.35	13.36	7.35
Dive bout duration (s)	1,296	334	1,878**	298	825	323	1,070*	434
N dives per bout	5.05	2.48	4.62	2.00	3.31	1.41	3.00	1.60

Mixed-factor models: sex = fixed factor, individual = random factor.

[a] These excluded preceding dives to bout intervals in murres (female: N = 1,318, male: N = 1,464) and razorbills (female: N = 697, male: N = 316).

Table 3.3 Thick-billed murres. Mixed-factor model comparisons of standardized depth-by-depth data (Rolf & Sokal, 1998) of male ($N = 14$) and female ($N = 16$) dive parameters, so differences are independent of depth. Statistical differences when $P \leq 0.05$.

	Female ($N = 1,721$)		Male ($N = 1,927$)		Statistics	
					F	P
	Mean	SD	Mean	SD	(df = 1, 28)	
Dive Duration	0.115	0.841	0.129	0.906	0.001	0.981
Bottom time	-0.054	0.827	0.279	0.898	3.205	0.084
Ascend rate	0.078	1.057	0.024	0.995	0.034	0.855
Descend rate	-0.212	0.936	0.186	1.031	2.881	0.101
Post-dive interval [a]	-0.189	0.076	-0.227	0.116	9.958	0.004
Dive cycle [a]	-0.116	0.778	-0.106	0.863	0.005	0.945
Diving efficiency [a]	0.160	0.825	0.513	0.769	3.827	0.060

Mixed-factor models: sex = fixed factor, individual = random factor.

[a] These excluded preceding dives to bout intervals (female: $N = 1,318$, male: $N = 1,464$).

3.4.2.1 *Murre dive profiles in relation to prey type*

Murre's dives were mostly W-shaped (59%) and U-shaped (31%), and to a lesser extent square-shaped (5%), V-shaped (3%), or other asymmetrical shapes (3%). The number of W-shaped and U-shaped dives varied according to dive depth in opposite directions. The proportion of W-shape dives decreased with depth whereas the proportion of U-shape dives increased with depth (Fig. 3.5). Shallow W-shaped dives were significantly shorter

in duration ($F_{[1, 65.33]} = 69.26$, $P < 0.0005$), and had slower descent rates ($F_{[1, 75.79]} = 24.65$, $P < 0.0005$) than U-shaped dives. Log-PDI was significantly shorter in W-shaped dives than U-shaped dives (mixed-factor model: $F_{[1, 68.44]} = 39.42$, $P < 0.0005$). Diving efficiency was significantly higher in W-shaped dives than U-shaped dives (mixed-factor model: $F_{[1, 64.41]} = 18.25$, $P < 0.0005$; Table 3.4). These differences in dive parameters between dive profiles may indicate specific methods of capture for various prey species of males and females.

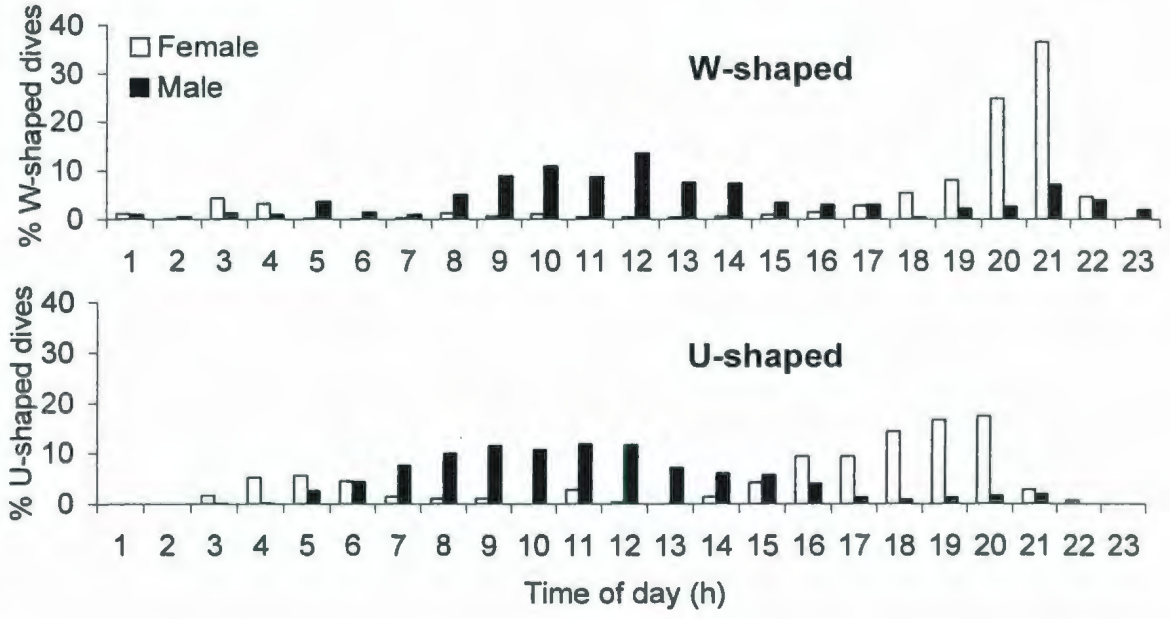


Figure 3.6 Hourly variation in the frequency of W- and U-shaped dives of male and female thick-billed murre at Gannet Islands, Labrador.

Table 3.4 Statistical comparisons of parameters of W-shaped and U-shaped between male and female thick-billed murres. Asterix (*) denotes significance between groups.

	U-shape						W-shape					
	Female		Male		Total		Female		Male		Total	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Dive Depth (m)	40.66	25.66	45.33	20.79	44.15*	22.14	13.4	7.67	21.45*	11.77	16.59	10.29
Dive Duration (s)	136.2	61.18	138.3	44.64	137.8*	49.29	75.02	26.15	97.07*	26.87	87.77	28.55
Bottom time (s)	46.20	24.82	48.05	18.11	47.58	20.51	32.57	12.11	45.54*	14.30	37.71	14.59
Ascend rate ($m\ s^{-1}$)	0.735	0.252	0.886	0.265	0.85	0.27	0.549	0.205	0.761	0.291	0.63	0.26
Descend rate ($m\ s^{-1}$)	0.911	0.281	0.991	0.213	0.97*	0.23	0.703	0.246	0.759	0.236	0.73	0.24
Post-dive interval (s) [a, b]	56.62	4.64	66.54	3.188	64.14*	3.50	22.70	10.30	34.77	6.09	26.85	8.62
Dive Efficiency [a]	0.267	0.116	0.270	0.119	0.27	0.12	0.348	0.121	0.357	0.113	0.35*	0.12

[a] These excluded preceding dives to bout intervals (females: $N = 1{,}032$, males: $N = 669$)

[b] Data were log (Base 10)-transformed before the analysis (CV instead of SD is shown in the table).

Thick-billed murres delivered to their young mainly daubed shanny (*Lumpenus maculatus* ; 83% by number, $N = 956$), followed by capelin (*Mallotus villosus;* 10%). All other prey species, such as sandlance (*Ammodytes sp.*), blennies (*Lumpenus sp.*), eelpout (*Lycodes sp.*), Arctic cod (*Boreogadus saida*), and invertebrates added up to only 7% of prey delivered to chicks. We observed three cases of crustaceans, which were delivered by females only at about 05:00 h in the morning.

Prey fed to chicks differed significantly between the sexes ($\chi^2_{[2]} = 13.91$, $P = 0.016$). Both sexes fed their chicks mainly daubed shanny (males: 82%, $N = 441$ items, females: 84%, $N = 515$ items), however males provided significantly more capelin than females (12% vs. 7% respectively, $\chi^2 = 6.96$, $P = 0.008$, Fig. 3.7).

We assumed that the prey item delivered to the chick was caught on the last dive. The last dives corresponding to daubed shanny delivery were mostly U-shaped (77 %, $N = 13$), the rest were single dives of square-shaped, V-shaped, and asymmetrically-shaped. Half of the last dives followed by capelin delivery ($N = 4$) were U-shaped and half were square-shaped. No prey deliveries to chicks followed W-shaped dives.

3.4.3 Razorbill diving behaviour

The maximum depth recorded for razorbills was 36 m (160 s) and 27 m (90 s) for females and males respectively. Razorbills dived deeper at times when total illumination

was higher (Figure 3.2). Depth of razorbills' dives was affected by time of day (mixed-linear model: $F_{[17, 1511]} = 11.73$, $P < 0.0005$, Fig. 3.2). However, male and female depth of dive was affected differently by time of day (sex*time: $F_{[1, 1511]} = 9.183$, $P < 0.0005$). By analyzing the sexes independently, we found that the dives of females were significantly shallower at 04:00 h (Post-hoc Tukey HSD test: $P < 0.003$) and deeper between 11:00 h and 12:00 h than other times of the day (Post-hoc Tukey HSD test: $P < 0.008$). These times coincided with lowest and highest illumination levels at Gannet Islands (Fig. 3.2). In contrast, the depth of male razorbills' dives did not differ significantly among hours (Post-hoc Tukey HSD test: $P > 0.05$). We excluded 3 hour-periods (04:00 h, 20:00 h, and 21:00 h) in the post-hoc analysis for males because of small sample size.

Razorbills started and finished foraging at 04:00 h and 22:00 h respectively; very few dives were recorded after dark (Fig. 3.2). There was not a clear division of foraging times between sexes, males and females foraged throughout the day. Nevertheless, about half of the dives of females were concentrated at morning hours (04:00 – 08:00 h), while 58% of males' dives occurred at mid-day and early afternoon hours (13:00 –17:00 h, Fig. 2). At twilight periods, females performed more dives around dawn (03:30 – 05:30 h, 31%) than around dusk (20:00 – 22:00 h, 10%; fig. 3.1). Overall, males performed fewer dives around dawn (9%) and dusk (0.8%), respectively, than females.

A multivariate mixed-factor analysis of the main razorbill dive parameters (depth, duration, ascent and descent rates, and bottom time) indicated that diving behaviour

differed by sex in razorbills (MANOVA: Wilk's Lambda = 0.948, $F_{[5, 7]} = 12.46$, $P < 0.005$). The univariate mixed-factor analysis of depth and other dive parameters showed no significant differences between sexes (mixed-factor models: $P > 0.05$; Table 3.2), except for bottom time (mixed-factor model: $F_{[1, 7]} = 8.224$, $P = 0.020$). The mean dive depths of both sexes were within the 95% confidence limits of the grand mean of depth (9.78 -10.43 m), although males were close to the upper bound limit. The mean values of males were above the upper bound of the 95% confidence limits of the grand mean of dive duration (4911-50.80 s) and ascent rates (0.60 – 0.62 m/s), which indicate a type II error.

There were significant differences in the number of dives performed by females and males (10 m-interval depth categories, Chi-square: $\chi^2_1 = 60.933$, $P < 0.0005$, Fig. 3.3). Female razorbills performed more dives less than 10 m in depth (61%), and males performed more dives greater than 10 m (58%, Fig. 3.3). There were significant differences in the distribution of dive types for males and females ($\chi^2_{[4]} = 147.34$, $P < 0.0005$). Males had significantly more U-shaped and square-shaped dives than females, and females had more W-shaped dives than males ($\chi^2 = 144.97$, $P < 0.0005$, Table 3.1). No sex differences were found in the proportion of V-shaped dives or other asymmetrical dives ($\chi^2 = 2.27$, $P = 0.14$). V-shaped dives (11.9 ± 5.9 m) were significantly deeper than W-shaped (8.8 ± 5.4 m) and U-shaped dives (9.6 ± 4.4 m, mixed-factor model: $F_{[2, 28.7]} = 4.08$, $P = 0.028$) in razorbills. No differences in dive depth were found between W-shaped and U-shaped dives (Post-hoc Tukey HSD test: $P = 0.20$).

Between sexes, no differences were found in any dive parameter of the three dive shape categories (mixed-factor models, $P > 0.05$), except for bottom time. V-shaped dives (19.2 ± 4.4 s) and W-shaped dives (22.9 ± 5.7 s) of razorbill males had longer bottom times than those of females (V-shape: 17.7 ± 3.6 s, mixed-factor model: $F_{[1, 8.41]} = 8.34$, $P = 0.02$; W-shaped: 20.2 ± 5.9 s; $F_{[2,16.64]} = 5.07$, $P = 0.004$).

Dive duration correlated with depth (duration = 4.15 m/s depth + 0.29 s; $r^2 = 0.74$, $P = 0.001$; Fig. 3.5) and post-dive interval (PDI = 8.786 s + 0.31 duration, $r^2 = 0.19$, $P < 0.001$) in males and females. Despite slight differences in depth between the sexes, there were no intersexual differences in PDI, dive cycle and diving efficiency (mixed-factor model: $P > 0.05$, Table 3.2). The mean values of both sexes were within the 95% confidence limits of the grand means for each variable.

Males had longer bouts than females (mixed-factor model: $F_{[1, 7]} = 8.416$, $P = 0.023$); but they did not differ in the daily number of dives (mixed-factor model: $F_{[1, 7]} = 0.773$, $P = 0.409$) or bouts (mixed-factor model: $F_{[1, 7]} = 4.815$, $P = 0.064$). Likewise they did not differ in the number of dives per bout (mixed-factor model: $F_{[1, 7]} = 0.024$, $P = 0.881$; Table 3.2). The mean values of the sexes were within the 95% confidence interval limits of the grand means of bouts per day, dives per day and dives per bout.

3.4.3.1 *Razorbill dive profiles in relation to prey type*

Most dive profiles of razorbills were V-shaped (42%) and W-shaped (32%), and to a lesser extent U-shaped (11%), square shaped (2%) and other asymmetrical shapes (14%). The proportion of V-shape dives increased with depth and the proportion of W-shaped dives tended to decrease with depth (Fig. 3.5). The proportion of U-shaped dives did not vary with dive depth in razorbills (Fig.3.5). The proportion of V-shape dives increased with depth and the proportion of W-shaped dives tended to decrease with depth (Fig.3.5). Dive duration did not differ between the three dive categories (V-shaped: 51.9 ± 14.9 s, W-shaped: 47.7 ± 14.6 s, U-shaped: 50.8 ± 9.3 s, mixed-factor model: $F_{[2, 31.1]} = 0.96, P = 0.39$). U-shaped dives (25 ± 5.5 s) and W-shaped dives (20.7 ± 5.0 s) had significantly more bottom time than V-shaped dives (18.2 ± 3.9 s, mixed-factor model: $F_{[2, 40.95]} = 16.53, P < 0.0001$). Bottom times of U-shaped dives were significantly longer than W-shaped dives (Post-hoc Tukey HSD test: $P < 0.0001$). No differences were found among the three dive shapes in other dive parameters or PDI (mixed-factor model; $P > 0.05$). Dive efficiency was significantly higher in U-shaped dives (0.38, $CV = 1.14\%$) than W-shaped (0.34, $CV = 2\%$) and V-shaped dives (0.27, $CV = 3.3$ %, square-root transformation: mixed-factor model: $F_{[2, 32.41]}$: 12.56, $P < 0.0001$). W-shaped dives were significantly more efficient than V-shape dives (Post-hoc Tukey HSD test: $P < 0.0001$).

Razorbills delivered mainly sandlance (85% by number, $N = 1\,685$) and less frequently capelin (8%), daubed shanny (6%) and "other" species (1%) such as blennies (*Lumpenus sp.*), eelpout, Atlantic cod (*Gadus morhua*) and crustaceans. The composition of prey species delivered to chicks at the breeding site did not differ between male and female razorbill parents ($\chi^2_{[3]} = 6.69, P = 0.08$). Both sexes fed their chicks primarily

sandlance (females: 85%, $N = 884$, males: 84%, $N = 548$), and although males delivered more capelin (10%) than females (7%), this difference was not statistically significant ($\chi^2 = 3.48$, $P = 0.07$, Fig. 3.7).

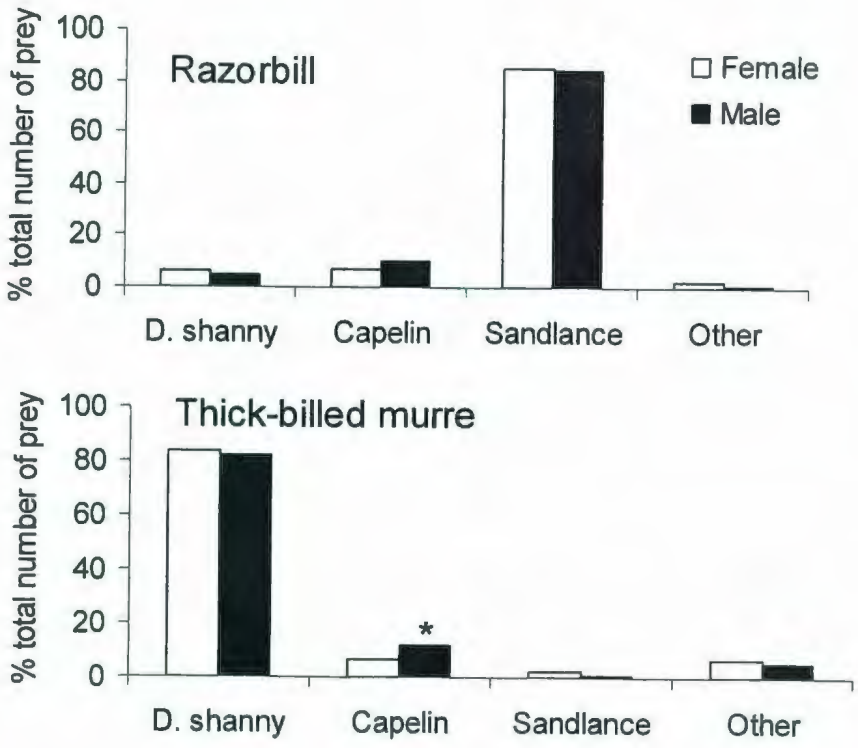


Figure 3.7 Prey species delivered by male and female thick-billed murres (males: 441 items; females: 515 items) and razorbills (males: 548 items; females: 884 items) at Gannet Is. Asterix (*) denotes statistical differences between sexes (Chi-square: $P = 0.008$).

3.5 DISCUSSION

3.5.1 Effect of time-depth recorders in birds' behaviour

The effect of experimentally-attached gear on seabirds is a neglected subject, yet the effects may be significant. Murres equipped with TDRs were shown previously to experience a reduction of body mass, parental effort (provisioning and brooding) and foraging trip duration (Paredes *et al.* 2005). In razorbills, no sex differences were found in initial body mass and daily rates of weight loss during the TDR deployment period. No data was available for the effect of instrumentation on razorbill's parental and foraging behaviour. However, we assumed that both murres and razorbills were negatively affected by the extra work of carrying TDRs. These behaviours are likely to be due to a reduction of birds' diving and/or flying performance, so we are aware that our measurements are likely under or overestimates. Nevertheless, because male and female thick-billed murres and razorbills are only slightly different in mass and morphometrics (Gaston and Jones 1998), and were treated identically in our procedures, we assumed that sex differences in foraging behaviour would occur as a result of naturally different strategies and not due to the effect of attached devices. In fact, males and females of both species did not differ in the number of dives per bout and per day and both were able to

dive to similar maximum depths, which suggested no differential TDR effect on the sexes underwater.

3.5.2 Patterns and differences in diving behaviour of sympatric thick-billed murres and razorbills

As previously reported, we also found that U- and V-shaped dives characterized time-depth profiles in thick-billed murres (Croll *et al.* 1992) and razorbills (Benvenuti et al. 2001; Dall'Antonia *et al.* 2001; Watanuki *et al.* 2006) respectively. Furthermore, we found that W-shaped dives were also common in both murres (59%) and razorbills (32%). U- and W- shaped dives represent different prey-capturing strategies in penguins, with prey pursuit occurring predominantly during the ascent and bottom phases, respectively (Kirkwood and Robertson 1997; Ropert-Coudert *et al.* 2000). Occurrences of W-shaped dives decreased with depth (i.e., more frequent at < 30 m); and U-shaped dives increased with depth (i.e., more frequent at > 50 m) in murres and razorbills. The fact that the same relationship between dive depth and dive shape was found in two species that use different parts of the water column (murre dive range was 4 -102 m compared to razorbill dive range 3 -36 m) supports the idea that the visual classification of dive profiles were not biased by the difference in maximum depth. The resolution of the diving program allowed for distinguishing zig-zags (W-shaped dives) from small wiggles at different depths clearly. In Peruvian boobies, U-shaped dives also increased with water depth (Zavalaga *et al.* 2007). W-shaped dives were more effective, diving

efficiency calculated as the proportion of the bottom time over a complete dive cycle; than U-shaped dives in thick-billed murres. Similar results have been reported for king penguins; W-shaped dives were more effective than U-shaped dives and ocurred more often at twilight periods probably for capturing crustaceans (Pütz & Cherel 2005). Crustaceans (e.g., euphausiids) swim within dense uni-directional and regularly spaced schools, but they do not have any specialized anti-predator behaviour as fish schools do (Hamner & Hamner 2000). Wilson *et al.* (2002) proposed that predators should be able to spend longer time at the bottom of a dive when feeding on smaller prey (crustaceans) than on larger prey (fish) because of differences in swim speed. In our study, analysis of the last dive in relation to prey delivered to chicks showed that W-shaped dives never preceded chick-feeding, suggesting they were used mostly for self-feeding. The analysis of dive type in relation to prey species suggested that U-shaped dives in thick-billed murres were used for capturing daubed shanny and capelin. Although our results are not conclusive because we were unable to obtain a large sample of prey deliveries by TDR-equipped murres ($N = 20$), other seabird studies support our findings. In thick-billed murres, U-shaped dives preceded deliveries of daubed shanny (Elliot *et al.* 2008) and preceded regurgitations of capelin in northern gannets (Garthe *et al.* 2000). At Gannet Islands, thick-billed murres and razorbills overlap in secondary prey items, thus it is likely U-shaped dives were performed by both species when capturing mid-bottom fish species, and W-shaped dives when capturing crustaceans.

V-shaped dives in razorbills and other shallow flight-divers such as northern gannets (Garthe *et al.* 2000), Peruvian Bobbies (*Sula nebouxii*; Zavalaga *et al.* 2007) and

rhinoceros auklets (Kuroki *et al.* 2003) could not be explained by constraints in aerobic dive limits as has been proposed for deep diving species (Schreer *et al.* 2001). The fact that sandlance was the main prey species delivered by both razorbill sexes, and that both sexes also had similar frequencies of V-shaped dives in this study suggested that this dive type was a result of a specific method of capture underwater. Sandlance schools preferred shallow-habitats (Ostrand *et al.* 2005) and characteristically form a tight ball when attacked (Grover & Olla 1983). While this behaviour may be an anti-predator response to reduced chances of individual mortality (see Hamilton 1971), it can also make the group more vulnerable near the surface to aerial predators (see review by Willson *et al.* 1999). We hypothesize that razorbills foraging at daylight were able to localize their prey from the air or sea surface, dive directly to the school and capture individuals on their way back to surface, helped by their positive buoyancy (threshold limit: 20 m; Watanuki *et al.* 2006). Other alcids can use buoyancy to enhance acceleration in capturing prey above the birds in the water column (Burger *et al.* 1993). This may allow for a faster return to the same feeding spot. The fact that razorbills have consecutive dives at similar depths within a bout (Dall'Antonia *et al.* 2001) supports this hypothesis.

According to niche theory, species must partitioning resources to be able to co-exist (Hutchinson 1978). Inter-specific competition for resources between thick-billed murres and common murres are likely to occur because of their similar size and foraging strategies during reproduction (deep divers and single-loaders). At Gannet Islands, they

differ in population size, thick-billed colony is considerably smaller than that of common murres 1:20). Although, these two species overlap in secondary prey species (i.e. capelin and daubed shanny) they deliver mainly one prey (Bryant & Jones 1999). The other two auks, razorbills and Atlantic puffins (shallow divers and multiple loaders) deliver mainly sandlance but with different stages of development: adult (razorbill; this study) and larvae (Atlantic puffins; Baillie & Jones 2003). Stable-isotopes studies indicate different distances to feeding areas during reproduction; thick-billed murres travel to farther areas than common murres, and razorbills stay near shore (Thompson *et al.* 1999). Thus, sympatric auks' partitioning of food resources may occur at Gannet Islands by different use of the water column, distances to feeding areas and primary prey or/and size (adult vs. larvae).

3.5.3 Sex differences in diving behaviour and inter-sexual patterns in murres and razorbills

In razorbills, dive depth varied with light intensity, being deeper at mid-day and shallower around dawn and dusk. Diving was infrequent at night. However, this pattern was mainly observed in female razorbills, which seem to track the diurnal patterns of sandlance. This shallow prey species is light sensitive and stays under the sand during the night and emerges and roams in the water column during daytime (Winslade1974; Hobson 1986; Ostrand *et al.* 2005). Male razorbills did not differ in dive depth

throughout the day (except twilight), and tended to deliver more secondary prey species, e.g., capelin, than females. Capelin is a pelagic fish that moves in schools at variable depths of the water column (Montevecchi & Piat 1986; Davoren *et al.* 2006) and typically follows the vertical migration of zooplankton at night (see review Mowbray 2002). Contrary to the behaviour at Gannet Islands, razorbill females at Skomer Is. delivered more secondary prey species (sprats) than males (Wagner 1997). The maximum depth for razorbills at Gannet Islands was 36 m and agreed with previous studies (reviewed by Hipfner & Chapdelaine 2002). However, the fact that razorbills can dive as deep as 140 m (Jury 1986) suggests light intensity may not be a limitation for this species. Thick-billed murres' diving behaviour did not closely track the diurnal pattern of light intensity and the sexes differed in the amount of secondary prey species as well. Although both sexes dived shallower at twilight, they dived deeper at different times of day regardless of light levels. Deep diving (up to 120 m) coincided with peaks of chick provisioning for each sex (Paredes *et al.* 2006), which likely targeted daubed shanny (benthic fish) the main prey delivered to murre chicks at Gannet Islands (Bryant & Jones 1999; this study). Both male murres and razorbills appeared to deliver more capelin than females. During the breeding season of auks mature capelin are found at sites near shore (< 50 m depth), probably due to spawning behaviour, while other age classes were found at intermediate (50-100 m) and deeper depths (up 250 m) off Newfoundland (Davoren *et al.* 2006). Stable isotope analysis suggested that breeding razorbills have a stronger tendency to feed in near shore waters than thick-billed murres (Thompson *et al.* 1999). Thus, male razorbills were likely feeding on spawning shoals of capelin at depths up to

30 m, while male thick-billed murres were likely foraging on deeper shoals of capelin off shore. On the other hand, the shallowest dives observed in both species at twilight and night may be the result of feeding on species that follow the vertical migration of zooplankton (i.e., crustaceans), and is likely for self-feeding (Chapter 4). Incubating murres dived shallower than chick-rearing murres at Hakluyt (77° 26'N; Benvenuti *et al.* 2002), suggesting differences in foraging for provisioning and self-feeding. Altogether, these results suggest diving behaviour in razorbills and murres were determined by the behaviour of the prey, which may largely depend on times and places each sex foraged for either provisioning or self-feeding.

Sex differences in dive parameters and timing of diving behaviour were found in both thick-billed murres and razorbills at Gannet Islands, although a less clear division between sexes in foraging times and dive depths occurred in razorbills (consistent with other studies; Wanless and Harris 1986; Wagner 1992). Among murres, the sex difference in dive depth could be attributed to the consistent differences in breeding site attendance and foraging schedules of each sex (Jones *et al.* 2002; this study). When dive depth was controlled differences in other dive parameters such as dive duration, ascent and descent rates, bottom time and post-dive interval disappeared, which suggest that sexes do not differ on the way they feed at the same level of the water column. In razorbills, the multivariate approach that combined the main dive parameters (depth, duration, bottom time, ascent rate and descent rate) suggested that diving behaviour depended on sex. However, we did not find significant differences in mean depths and

other dive parameters, except for bottom time, between the sexes using the univariate approach. The lack of significant differences between sexes in most of the dive parameters was probably due to the small sample size of razorbill males ($N = 3$; Type II error). Males' mean values of depth, duration, and ascent rate were above the upper bound of the 95% confidence limits of the grand means. These results suggest males' tendency for diving at deeper levels than females. In fact, we found female razorbills tend to forage at twilight periods (mainly sunrise) and dive to shallower depths more often than males (61% vs. 42% of total dives) as occurs with female murres. The fact that female razorbills had shorter bout duration than males, despite similar number of dives per bout, supports their more frequent shallow diving. Thus, it seems female murres, and to lesser extent, female razorbills take advantage of the vertical migration of crustaceans to shallow depths during twilight periods at Gannet Islands. This behaviour may allow for faster self-feeding rates and consequently a more efficient provisioning (Chapter 4). Although we observed few cases of crustacean delivery to chicks (murres 0.3 %, and razorbills 0.4%), the consistent reddish coloration of the guano that covered the ledges in the murre colony suggests crustaceans are a main part of adult diet there and at Coats Island (Croll *et al.* 1992). Crustaceans are also an important part of adult murre and razorbill diets, especially in the winter (Mehlum et al. 1996; Mehlum 2001; Hipfner and Chapdelaine 2002; see also Rowe *et al.* 2000).

Sex differences in foraging trip duration found in murres and razorbills at Gannet Islands (Paredes *et al.* 2006) may be partially accounted for by differences in diving activity. Dive duration and PDI decreased with depth in both species, which implied that

females should have shorter dive cycles (dive duration plus PDI) if they dive shallower than males. This explains how sexes performed similar numbers of dives per bout but females had shorter bouts than males. Thus, although sexes had similar numbers of dives and bouts per day females seemed to spend less time underwater than males, which may partially explain differences in trip duration.

Different distributions of dive shapes found between males and females seem to mirror differences in their diets and the different vertical distribution of the various prey species. Both female murres and razorbills performed significantly more W-shape dives than males. Between sexes, we found that W-shaped dives of female murres were shallower and shorter than those of males and had shorter bottom times, slower ascent/descent rates and shorter PDIs. These results are consistent with the different foraging times of males and females and diel vertical migration of their prey (i.e. crustaceans). Breath-holding divers experience changes in buoyancy resistance because of the compression of air in their respiratory system, feathers or hair (Lovvorn and Jones 1991; Wilson *et al.* 1992b). Alcids experience greater buoyancy since they have 1.4 times greater air volume per mass than penguins (Wilson *et al.* 1992b). Reduced buoyancy (threshold limit: 18-20 m, zero buoyancy: 62 m; Lovvron *et al.* 1999) of male murres at their depth range may allow them to spend longer time at the bottom of individual dives. Interestingly, we found that the efficiency of W-shaped dives did not differ between sexes, which supports the possible relationship between dive shape and prey species. Males of both species performed more U- shaped dives than females, consistent with a higher consumption of capelin than females. Similarly, the lack of difference in U-shape

dive parameters of murre males and females suggested the capture strategies of both sexes for prey at deeper levels of the water column were indistinguishable. The narrow range in dive depths may be why sex differences did not occur in the most dive parameters of the main dive profiles, W and V- shapes of razorbills.

3.3.4 Do parental roles determine foraging patterns and consequently diving behaviour?

We hypothesized that sex differences in diving behaviour could result from differences in foraging schedules determined by different parental roles of males and females at the Gannet Islands. As a result, sexes would forage under different at-sea environmental conditions (i.e. light levels or prey availability), which would in turn affect their dive depths and prey taken (Wilson *et al.* 1993; Jones *et al.* 2002) differently. The relatively similar inter-sexual segregation in feeding time and dive depth found in the two sympatric alcid species suggest that the observed foraging patterns were linked to the patterns of parental roles found at the Gannet Islands. We proposed that foraging schedules were driven by the need of males to be at the breeding site at times of higher chick vulnerability because of the greater ability of males to protect the chick (Paredes et al. 2006, Paredes and Insley unpublished data). In both species, males spend more nights with the chick than females (Paredes *et al.* 2006), suggesting that males were present at the breeding site during twilight periods. Our results confirmed that females were more often diving at twilight periods (mainly sunrise in razorbills) and therefore males were

present at the breeding site. Higher predation and kleptoparasitism rates occur at times when seabirds return from feeding sites, which coincides with sunrise and sometimes sunset (Oro & Martinez-Vilalta 1994; St. Clair *et al.* 2001; Williams & Ward 2006). These behaviours may potentially increase chick vulnerability during aggressive encounters between con-specifics and hetero-specifics. One of the most distinctive life-history characteristics of the Alcini species is that the male is the caregiver that accompanies the chick to sea (Gaston & Jones 1998). Chick survival at departure, which mostly occurs at sunset, is a major constraint for these species (Gilchrist & Gaston 1997b). Males seem to be morphologically and behaviourally more capable of chick/egg defence because they have larger bills that can be used as weaponry and because they are more aggressive than females (Chapter 5). Thick-billed murres that defended eggs were able to reduce predation by glaucous gulls (*Larus hyperboreus*) in comparison to birds that did not (Gilchrist & Gaston 1997a). Thus, male presence at the breeding site at times when chick is most at danger (i.e. sunrise and sunset) would potentially benefit parents' fitness, and consequently determine foraging schedules.

The fact that different nest attendance schedules, i.e., males diving at night and brooding during the day, have been reported for thick-billed murres at Coat Islands (K. Woo, in Gaston & Hipfner 2000) may be explained by differences in daylight periods and colony size. Larger bird colonies have greater nest competition and per-capita fight rates than smaller colonies because either non-breeding floaters contest sites more persistently or more floaters visit larger colonies (Brown & Brown 1996; Davis & Brown 1999). If breeding site competition is a major constraint for larger thick-billed murre colonies at

Coat Island, then male presence through longer daylight periods (3 h more than at Gannet Islands) may be necessary to defend the breeding site and chicks against prospecting non-breeders. Comparative studies between localities with different environmental conditions (i.e. light availability) and similar productivity are needed to confirm two major and related questions. First, whether the patterns of parental roles found at Gannet Islands are general to these alcid species?, and second whether these roles are driven by the foraging behaviour of males and females during reproduction?

In conclusion, we found a relatively similar temporal segregation of the sexes in dive foraging time, dive depth and prey during reproduction in two monomorphic, sympatric and closely related auks. Females dived at twilight periods and at shallower depths on average than males, which was reflected in their dive profiles. We propose that the different foraging schedules, and consequently dive depths, were driven by the need for males to be at the breeding site at times of higher chick vulnerability because of their better capability of defending the offspring.

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CHAPTER 4: SEX-SPECIFIC DIFFERENCES IN FORAGING BEHAVIOUR OF THICK-BILLED MURRES: PROVISIONING VS. SELF-FEEDING

4.1 ABSTRACT

In theory, breeding animals can experience different constraints in terms of energy gain and expenditure when foraging to feed their offspring than to feed themselves. In several alcid species, females are the main food providers for chicks while males mostly defend the chick or nest. I tested whether these sexual differences in parental behaviours are reflected on the provisioning and self-feeding in thick-billed murres at Gannet Islands. Males self-feeding foraging occurred through daylight and mostly during (49% of total diving bouts) and in between provisioning trips (31% of total diving bouts). In contrast, females' self-feeding occurred during "self-feeding only" trips (91%) at twilight, which coincided with the vertical migration of zooplancton (i.e. crustaceans) to surface waters. As a result, females' dives for self-feeding were shallower (17.17 ± 2.17m vs. 28.50 ± 3.50 m) and ascend rates slower (0.54 ± 0.04 m s^{-1} vs. 0.66± 0.05 m s^{-1}) than males. This suggests males were foraging on the same mid-deep prey delivered to chicks, which may partially explain their higher delivery of capelin. Diving

for chick provisioning was deeper than self-feeding, irrespective of the sex (male: 62.91 ± 7.01 m, female: 52.98 ± 8.03 m) or the time of day. Number of dives and other parameters of chick provisioning bouts did not differ between sexes. Both results suggest similar diving effort of the sexes for parental tasks. Foraging trips and return time to the colony with meal delivery for females (1.53 h, 0.34 h) was significantly shorter than for males (6.63 h, 0.79 h), which suggested a division of foraging areas between sexes (estimated ranges: females 31 km; males 63 km). During a chick- provisioning foraging trip, females spent significantly less time underwater (0.27 h vs. 1.45 h) and flying/resting at sea (1.43 h vs. 4.61 h). Higher self-feeding rates and closer feeding locations may partially explain female's higher delivery rates at the breeding site. Altogether, my results indicate different strategies of males and females for self-feeding and provisioning foraging due to different energy and time constraints, which reflect on their parental roles.

4.2 INTRODUCTION

Parents must balance tradeoffs of resource allocation between survival and reproduction to maximize fitness (Williams 1966). Foraging determines an individual's intake of resources and its later energy expenditure in fitness-related activities. On the other hand, decisions about resource allocation in foraging activities will depend on the net income

and resource availability as well as other ecological and physiological factors (Boggs 1992). According to optimal foraging theory, foraging strategies have evolved to maximize fitnessl, which is a function of their foraging efficiency (Schoener 1971; Pyke *et al.*1977). During reproduction, most birds forage for self-feeding and provisioning their offspring. These should be taken as two different foraging processes because constraints on energy intake and expenditure may be different (Ydenberg 1994). Foraging behaviour may tend toward either rate maximization (time constraint) – or efficiency maximization (energy constraint) depending on the allocation of resources between self-feeding and provisioning (Ydenberg *et al.*1994).

Parents are expected to value food for self-feeding and offspring differently because although foraging in both cases is costly, self-feeding has short-term benefits (energy balance) while chick-provisioning has long-term benefits (to fitness) (Ydenberg 1994). Some evidence supports these predictions. For example, diet studies have shown that adults feed their chicks with larger or higher quality prey than those captured for themselves (Bradstreet & Brown 1985; Piat 1987; Mahon *et al.* 1992; Shealer 1998; Grieco 2002). Other studies have shown birds have different foraging behaviour and prey selection when feeding for their chicks than for themselves (Weimerskirch *et al.* 1997; Davoren & Burger 1998; Clarke 2001; Markmann e*t al.* 2004). Deeper dives have been reported for thick-billed murres rearing chicks than for those incubating eggs (Benvenutti *et al.* 2000); and longer dives for provisioning than self-feeding (Jones *et al.* 2002). Relatively few studies have considered possible differences between the sexes in these

two foraging processes (but see Weimerskirch *et al.* 1997, Jones *et al.* 2002; Markmann *et al.* 2004).

Thick- billed murres are pursuit-divers, central place foragers and single prey item loaders (Gaston & Jones 1998); so their foraging range is constrained by the requirement of returning to their breeding sites at regular intervals. Murres raise a single offspring, which departs with the male parent after 15 days of biparental care at the breeding site and completes its development at sea over the following 3-4 weeks (Gaston & Jones 1998). At the Gannet Islands, Labrador, both parents fed their chicks mainly with a benthic fish (daubed shanny, *Lumpenus maculatus*), however males provided more capelin (*Mallotus villosus*) than females. Males had longer but less frequent foraging trips with meal delivery than females (Paredes *et al.* 2006, Chapter 3). Males forage during the day at deeper depths than females, which foraging occur mostly at twilight periods (Jones *et al.* 2002; Chapter 3). These differences in diving and foraging behaviour seem to be result of the time at which each sex dive (Jones *et al.* 2002; Chapter 3). Sex differences in foraging for self-feeding and provisioning may also result from distinctive parental roles (Markmann *et al.* 2004). As thick-billed murres, other female auks such as the commom murre (*Uria aalge,* Wanless & Harris 1986; Wilhem 2004), the Atlantic puffins (Creelman & Storey 1991), the crested auklet (*Aethia cristatella*, Fraser *et al.* 2002), and the razorbill (*Alca torda*, Paredes *et al.* 2006), are mostly in charged of chick provisioning. In marblet murrelets, males' higher rate of nest visitation suggests their major involvement in provisioning (Bradley *et al.* 2002). Males dovekies provided more

meals per day (Harding *et al.* 2004) but less in quality and quantity than females (Wojczulanis *et al.* 2006). Foraging for chick provisioning is very costly, especially for murres because of their reduced flying efficiency (Gaston 1985; Gaston & Jones 1998). Therefore, it is possible females have different ways of foraging for chick-provisioning than males to compensate for associated energetic costs.

Murres usually perform a direct flight back to the colony for delivering a single fresh prey to their chicks (Benvenuti *et al.* 1998); which can allow distinguishing between foraging trips for provisioning and self-feeding and estimating distances to feeding areas.

My main goal was to test whether the different parental roles of male and female thick-billed murres are accompanied by differences in chick-provisioning and self-feeding foraging at Gannet Islands, Labrador. Specifically, I determined foraging trip durations, return time to the colony (distance to feeding areas), diving bouts and parameters; and prey species delivered by birds carrying time-depth recorders. I used this information to estimate the foraging effort of males and females at sea and the total parental effort allocation in the final chapter.

4.3 METHODS

The study was carried out during July and August 2000 and 2001 at a breeding colony of ca. 150 pairs of thick-billed murres ("Grey Cup", GC4) at one of the six Gannet islands located on the low arctic coast of Labrador, Canada (53°56′N, 56°32′W). During the study, sunrise and sunset occurred c. 03:30 and 21:30 local time respectively.

I instrumented a total of 40 birds (18 males and 22 females) with time-depth recorders (TDRs) as part of a general study of sex differences in diving behaviour (see chapter 2). Birds with TDRs had chicks between 1-11 days old at the time of capture.

We used two types of TDRs, MK7 (Wildlife Computers, 25 g, flat shape with pointed end) and LTD_100 (Lotek, 16 g, cylindrical shape with rounded end); both similar in size (5-8 x 1-2 x 1-2 cm), and in cross-sectional area (1.7-1.9 cm^2, 1.2-1.3 % of the body area). Data from both types of TDRs were pooled because there were no significnat differences in diving behavior between birds outfitted with these different TDRs (see chapter 2). Only one member of each pair was captured for TDR deployment while the other was brooding, so a chick was never left unattended. Birds were captured using noose poles from the edge of the cliff above the colony. Their mass was measured to the nearest 10 g using a spring scale. After weighing individuals were marked with permanent (stainless steel) and temporary (color) numbered bands. TDRs were attached to the back of feathers using three strips of black TESA® tape, cable ties and drops of cyanoacrylate glue ("hot stuff"®) under both ends of the device. Handling time from

capture to release totalled 5-8 minutes. Time and depth were recorded continuously at 5 sec interval during 1-4 days. After TDR recovery data were immediately downloaded to a laptop computer for analysis. Blood samples (0.5 ml) were taken from the tarsus vein and stored in vials with 95% ethanol for use later to determine the sex of each bird by molecular DNA analysis (Fridolfsson & Ellegren 1999).

Parental care behaviour of birds with TDRs was observed between dawn and dusk (0400-2200 h) from a blind located at the edge of the colony. All events of meal delivery and the departure and arrival of adults were recorded to identify foraging trips "with meal delivery" and "without meal delivery" and to differentiate diving bouts for chick-provisioning and self-feeding. Prey delivered by each parent was identified at the species level when possible. Because murres usually return in direct flights from the foraging areas to deliver a single fresh fish to their chicks (Benvenutti *et al.* 1998) I used a flight speed of 65 km. h^{-1} (Benvenutti *et al.* 1998) and the return time from the last dive at sea to the breeding sites, to estimate the maximum travel distance to foraging areas for each bird .

4.3.1 Data and statistical analysis

My approach combined two types of information: records of diving activities and behavioural observations of birds instrumented with diving data loggers.

Thirty of the 40 TDR attachments yield useful data; seven had anomalous data and 3 fell off the birds before re-capture. Twenty-three of the 40 TDR-equipped birds (11 females and 12 males) had both information of diving and parental behaviour and were used for the analysis of chick-provisioning and self-feeding foraging.

I grouped individual dives according to three types of bouts: all bouts before the last bout ("self-feeding") and last bout before returning to the colony either without meal delivery ("last bout without meal delivery") or with meal delivery ("chick-provisioning"). Trips were assumed to be for self-feeding when birds retun without food and when they did not return to the colony at the end of the day ("no return, overnight at sea").

Data were averaged by individual and sex before statistical analysis of type of bout and foraging trip. I reported the duration of individual dives but did not include this in any statistical analysis because there was a highly statistically significant correlation between depth and dive duration ($r^2 = 0.89$, $P = 0.001$; Chapter 2). Therefore, I assumed there were statistical differences in duration of dives when statistical differences were found in depth.

For the analysis of the effect of time of day on dive depth/duration I grouped dives into ten 2 h-periods (1 = 21:31-03:30, 2 = 03:31 – 05:30, 3 = 05:31 – 07:30, 4 = 07:31- 09:30, 5 = 09:31 – 11:30, 6 = 11:31 – 13:30, 7 = 13:31 – 15:30, 8 = 15:31 -17:30, 9 = 17:31 – 19:30, 10 = 19:31 – 21:30) according to sunrise (period 2) and sunset (period 10) occurrence.

I quantified the time-activity budget of males ($N = 8$) and females ($N = 11$) during foraging trips with chick meal delivery. Based on information from time-depth recorders and observations at the breeding site, I estimated the total time spent diving including self-feeding and chick feeding bouts ("time underwater"), and total time resting at sea or flying between bouts ("time at sea"). I assumed birds that remained at sea overnight (3/11 females and 1/8 males) started the first foraging trip at 3:30 am (sunrise) and only have return time flying to the colony. All data were averaged by individual and sex before statistical analysis.

Dive data were analyzed using the dive analysis program from IKNOS toolbox (Y. Tremblay, unpublished) developed with MATLAB software (The MathWorks, Natick, Massachusetts). The program was setup to analyze all dives equal to or exceeding 3 m deep (6 times the depth resolution of the instrument), and 15 seconds duration (3 times the sampling interval). Dive parameters were calculated for each dive, following Tremblay & Cherel (2003). These included maximum depth, duration, bottom time (the amount of time between 75% and 100% of the maximum depth reached), and descent and ascent rates for individual dives. Because 95% of dives had a post-dive interval less than twice their duration, this threshold was chosen as a bout ending criterion.

Statistical analysis was carried out using SPSS version 11.5. We used parametric tests (ANOVA, Student *t*-test) to compare groups if the residuals met the assumptions for the general linear model. If not, data were transformed and checked whether the residuals

met the assumptions for the transformed response variable. For instance, data of foraging trip duration were log-transformed before statistical analysis to reduce skewness and variance of the means. Chi-Square test with Yates's correction was used to compare proportions. Means were expressed ± SE of the mean. All comparisons were two-tailed, and differences were considered significant when $P \leq 0.05$.

4.4 RESULTS

4.4.1 Chick Provisioning and Self-feeding foraging quantified

Sexes foraged at different times of the day; males foraged mostly between late morning and early afternoon, and females foraged during early morning and late afternoon (Figure 4.1). The number of bouts per trip varied between 1 and 26 for females and 2 and 30 bouts for males. Males (11.9 ± 1.10 bouts trip $^{-1}$ day $^{-1}$; $N = 12$) had significantly more bouts per foraging trip than females (6.63 ± 1.18 bouts trip $^{-1}$ day $^{-1}$; $N = 11$; ANOVA: $F_{1,21} = 10.80$, $P = 0.004$). Often long self-feeding bouts preceded short bouts for chick provisioning and without meal delivery for both males and females. Female murres had most of their self-feeding bouts at the end of the day (Figure 4.1).

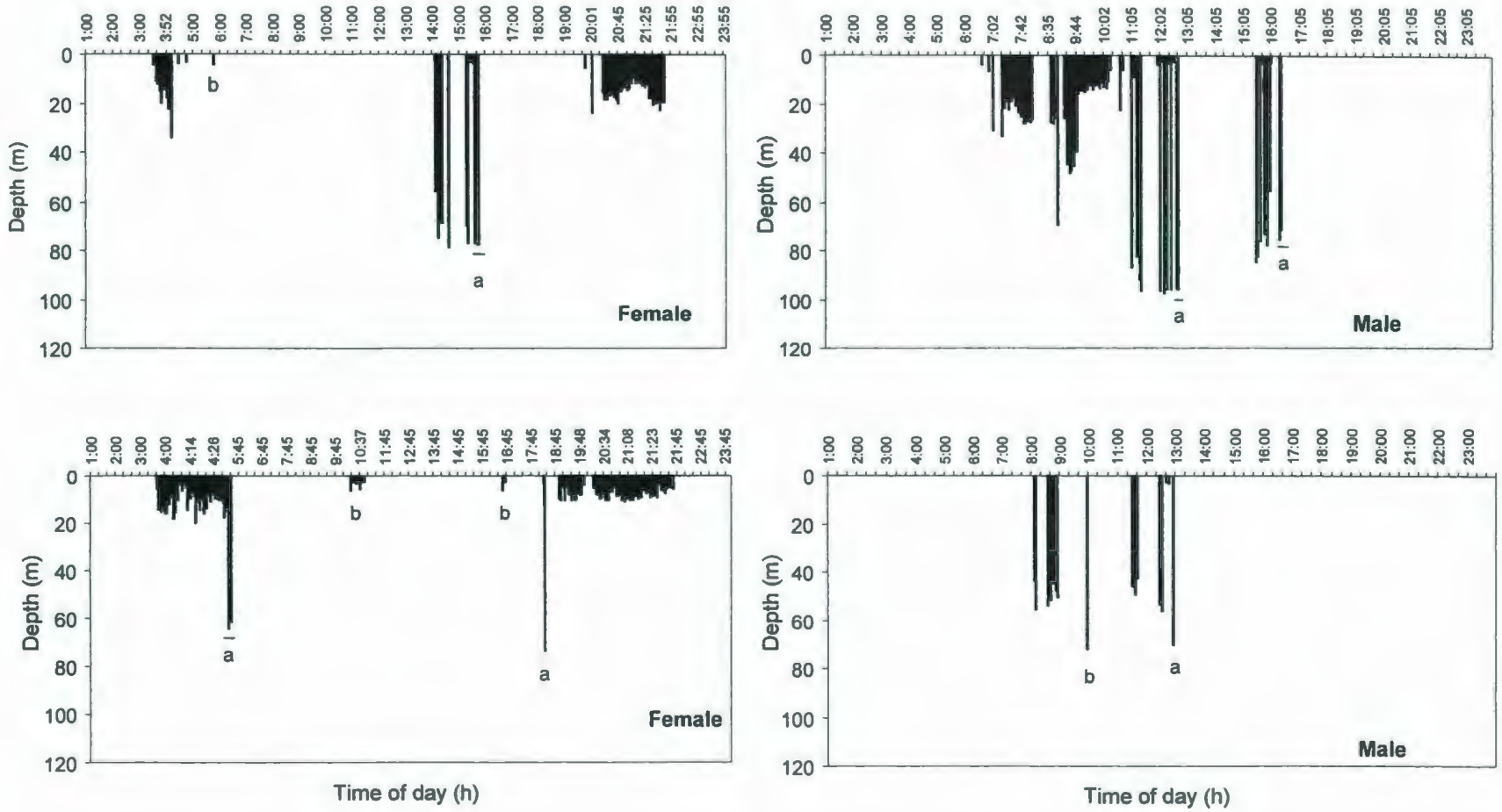

Figure 4.1 Dive profiles of two different male and female thick-billed murres according to time of day at Gannet Islands, Labrador. Letters indicate type of bouts: provisioning (a), last bout without delivery (b), and self-feeding bouts (all remaining dives)

The timing of females' foraging bouts for chick provisioning was bimodal with most bouts occurring early in the morning between periods 1 – 3 (73%, $N = 15$) and in the remainder occurring late in the afternoon between periods 6 – 8 (27%, Figure 4.2 a). The period with the most activity in the morning was period 1 (03:30 – 05:30 h, 40%), and in the afternoon was period 7 (15:30 – 17:30 h, 13%). The earliest dive for females' chick provisioning was at 04:55 and the latest at 19:07. Most males' bouts for chick provisioning occurred mid-day onwards, between periods 5 – 8 (90%, $N = 19$). The remainder of diving bouts by males (10%) occurred during periods 2 and 3 in the early morning. The earliest provisioning dives for males dive for provisioning occurred at 05:30 and the latest at 17:58. Neither sex dived for chick provisioning during periods 4 (09:30 –11:30) or 9 (19:30 – 21:30).

The timing of self-feeding bouts by females occurred mainly late in the afternoon, between periods 6 and 9 (80%, Figure 4.2 b). In contrast, self-feeding bouts by males occurred mostly during the day, between periods 2 and 6 (80%, Figure 4.2 b). The last bout before returning to the colony without meal delivery occurred similarly during all time periods for both males and females, except for a relatively high occurrence (38%) during period 1 for females (38%, Figure 4.2 c).

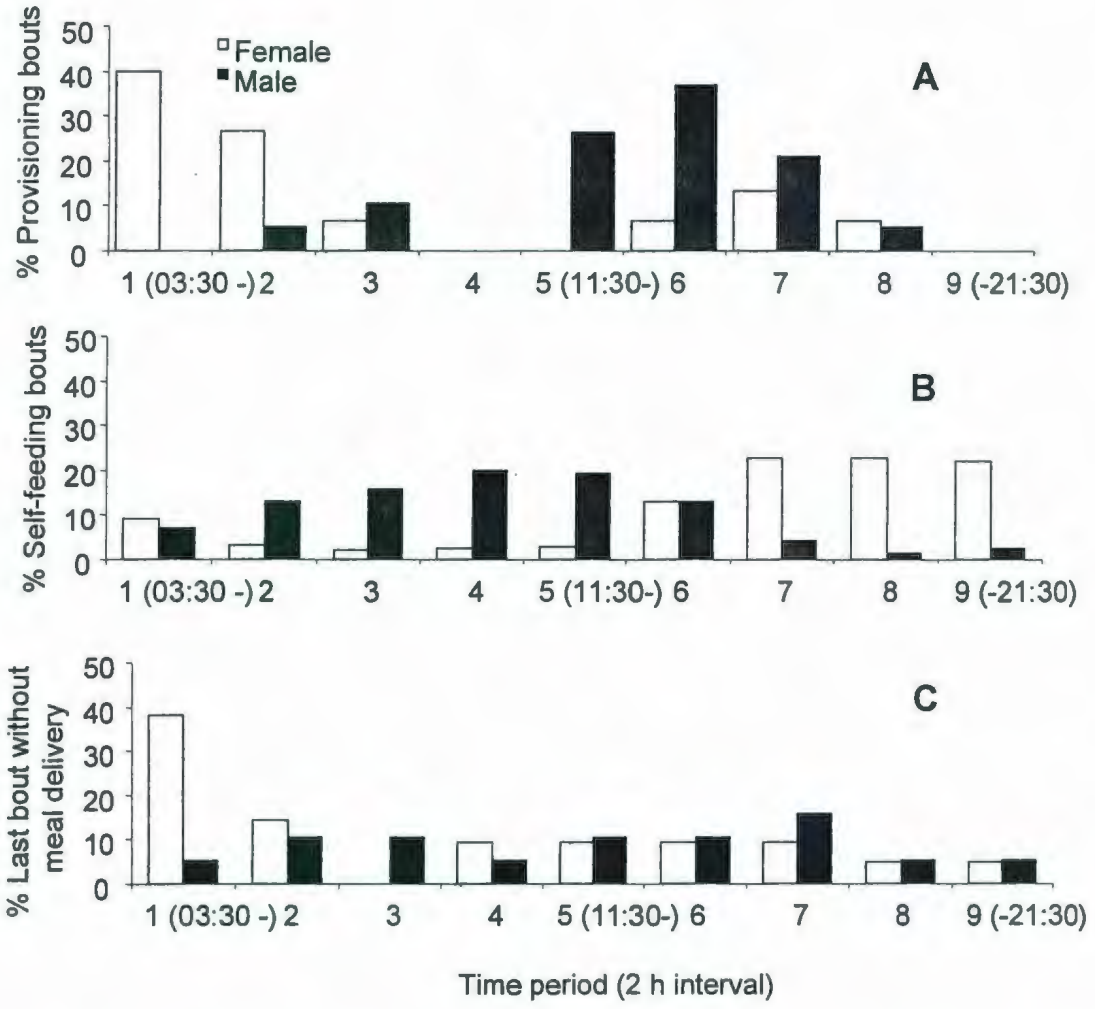

Figure 4.2 Daily proportion of type of dive bouts of female ($N = 11$) and male ($N = 12$) thick-billed murres according to 2 h-interval periods: Chick provisioning (a), Self-feeding (b), Last bout without meal delivery (c).

We found a significant effect of the type of bout (two-way ANOVA: $F_{2, 53} = 10.7$, $P = 0.0005$) on dive depth, but no effect of sex ($F_{1, 53} = 3.107$, $P = 0.084$, Figure 4.3 a) nor an interaction between sex and type of bout ($F_{2, 53} = 0.47$, $P = 0.63$). Post-hoc analysis of the type of bouts showed that both murre sexes dove deeper during bouts for

chick provisioning than for self-feeding or last bout without meal delivery (Tukey HSD, $P < 0.05$, Figure 4.3 a). No significant difference in dive depth was found between self-feeding and last bout without meal delivery (Tukey HSD, $P > 0.05$). Between sexes, males dove significantly deeper during self-feeding bouts than females (ANOVA: $F_{1, 21} = 10.8$, $P = 0.003$, Figure 4.3 a),but no sex differences were found in dive depth for the last bout without meal delivery or chick-feeding (ANOVA: $P < 0.05$). Within sexes, males (ANOVA: $F_{1, 19} = 5.9$, $P = 0.025$), and females (ANOVA: $F_{1, 17} = 19.02$, $P < 0.005$) dove deeper during chick-provisioning bouts than for self-feeding (Figure 4.3 a). The number of dives performed by individuals per day was affected by the type of bout (self-feeding: 66.1 ± 3.3 dives day $^{-1}$; chick-feeding: 3.2 ± 0.8 dives day $^{-1}$; last bout without meal delivery: 4.0 ± 0.8 dives day $^{-1}$; two-way ANOVA: $F_{2, 53} = 277.6$, $P < 0.0005$) but not by the sex of birds ($P < 0.05$). We found no interactive effect of sex and type of bout on the number of dives per day ($F_{2, 53} = 1.48$, $P = 0.24$).

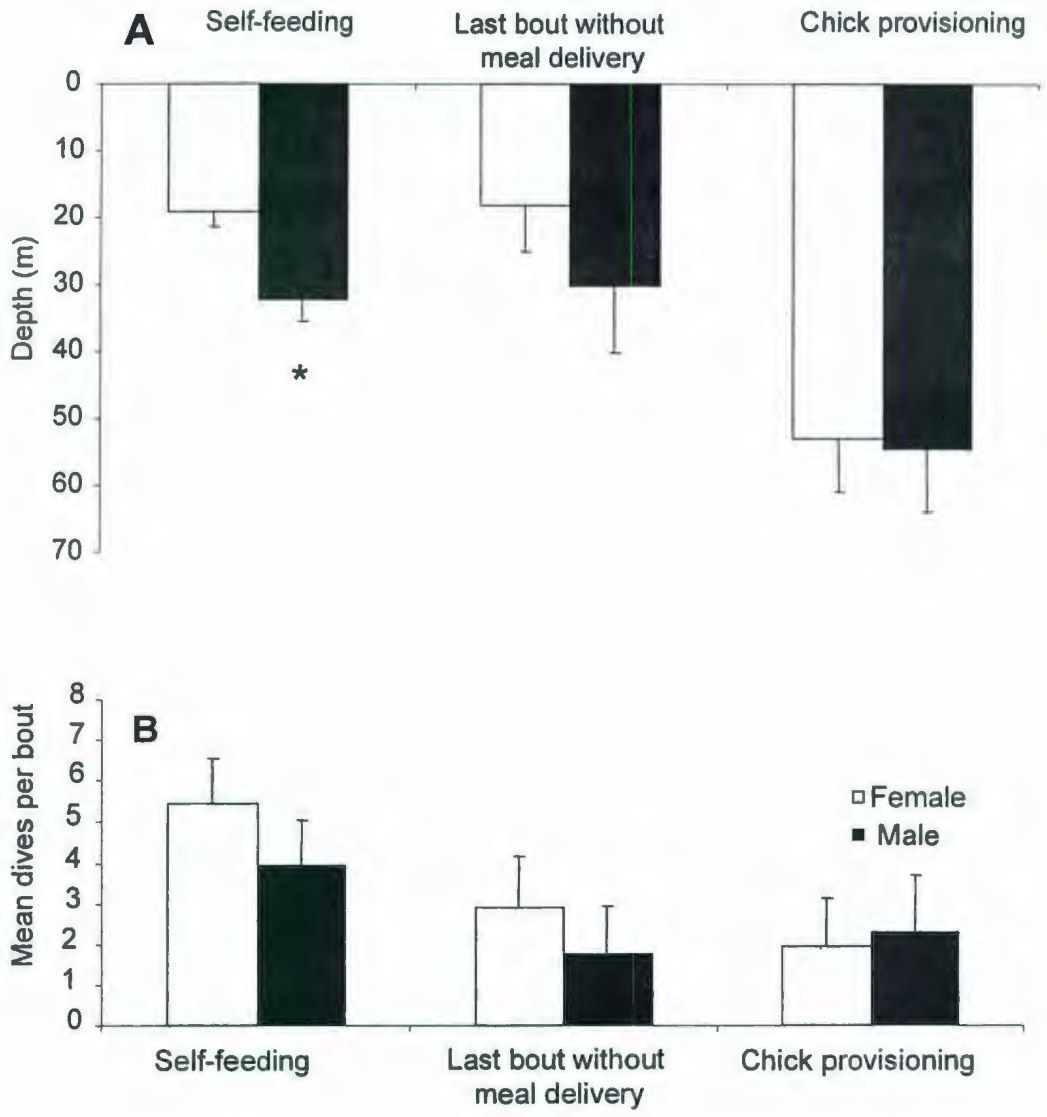

Figure 4.3 Differences in depth (A) and number (B) of individual dives of male ($N = 12$) and female ($N = 11$) thick-billed murres during chick provisioning bouts (last bout with meal delivery), self-feeding bouts (all bouts before the last one), and last bout without meal delivery. Means ± SE. Asterix (*) indicates statistical differences between sexes (ANOVAs, $P < 0.05$).

Similar results were found for the number of dives performed per bout. We found no difference between sexes (log-transformed data, two-way ANOVA: $F_{1,53} = 2.06$, $P = 0.16$), but a significant effect of the type of bout in the ($F_{2,53} = 11.37$, $P < 0.0005$; Figure 4.3 b). There was no effect of the interaction term sex* type of bout on the number of dives per bout ($F_{2,53} = 1.52$, $P < 0.23$).

For the rest of the diving analysis, I excluded the last bout without meal delivery because showed no clear pattern of behaviour.

Sexes differed on diving parameters (maximum depth, ascent and descent rates, and bottom time) during self-feeding bouts (MANOVA; Wilk's Lambda = 0.51, $F_{4,18} = 4.40$, $P = 0.012$) but not during chick-provisioning bouts (MANOVA; Wilk's Lambda = 0.925, $F_{4,12} = 0.090$, $P = 0.908$ Table 4.1). Parameters of self-feeding dives differ according to the two trip categories (provisioning vs. "self-feeding only trips": MANOVA: Wilk's Lambda = 0.53, $F_{4,16} = 2.89$, $P = 0.048$). Sexes differed on dive depth ($F_{1,20} = 6.70$, $P = 0.018$) and ascent rate ($F_{1,20} = 4.657$, $P = 0.043$) only during "self-feeding only" trips. On those trips that also included chick provisioning the sexes showed no differences in self-feeding dive parameters (MANOVA: $P > 0.05$; Table 4.1).

Table 4.1 Diving parameters (Mean ± SE) of male ($N = 12$) and female ($N = 11$) thick-billed murres during bouts for chick-provisioning and self-feeding. Asterix (*) denote statistical differences ($P < 0.05$).

	Chick-provisioning		Self-feeding		Pooled	
	Female	Male	Female	Male	Female	Male
Depth (m)	58.97 ± 6.17	62.0 ± 7.10	20.16 ± 2.45	32.45 ± 3.27*	35.25 ± 5.33	44.27 ± 4.73
Duration (s)	164.26 ± 9.10	163.02 ± 14.30	83.92 ± 5.22	104.47 ± 7.5*	115.16 ± 10.7	127.89 ± 9.6
Bottom time (s)	40.91 ± 4.65	42.14 ± 5.48	25.07 ± 1.77	26.76± 3.03	31.23± 2.75	32.9 ± 3.26
Ascent rate (m s^{-1})	0.82 ± 0.006	0.88 ± 0.006	0.54 ± 0.003	0.70 ± 0.004*	0.65 ± 0.004	0.77 ± 0.004*
Descent rate (m s^{-1})	0.99 ± 0.007	1.11 ± 0.006	0.62 ± 0.002	0.77 ± 0.004*	0.76 ± 0.005	0.90 ± 0.005*

We analyzed the effect of time of day on the depth of individual dives during self-feeding and chick provisioning bouts of males and females. As noted earlier, most self-feeding dives occurred during two periods: "twilight" (03:30 – 05:30 and 19:31– 21:30) and "daylight" (05:31–19:30). For self-feeding bouts, time of day ($F_{1, 138} = 6.58$, $P = 0.011$) and sex had an effect on dive depth (square-root transformed data: two-way ANOVA: $F_{1, 138} = 9.01$, $P = 0.003$). There were not an interaction effect of the main factors on depth (sex* time of day: $F_{1, 138} = 1.08$, $P = 0.301$). Both sexes dived shallower during twilight than during daylight periods (ANOVA: $F_{1, 140} = 11.395$, $P = 0.001$). Males dived deeper than females during daylight (ANOVA: $F_{1, 111} = 19.345$, $P < 0.0001$) but not during twilight periods (ANOVA: $F_{1, 28} = 2.406$, $P = 0.133$, Figure 4.4). Because the sexes differed in the timing of diving for chick-provisioning, we grouped feedings bouts of each sex into two time periods: "morning" (females: 03:30 – 09:30, $N = 9$, males: 05:31– 09:30, $N = 3$) and "afternoon" (females: 13:30 –19:30, $N = 4$, males: 11:30-19:30, $N = 13$) and analyzed the sexes' bouts independently. For neither males (Student's *t*-test: $t_{1, 14} = 1.34$, $P = 0.20$) nor females (Student *t*-test: $t_{1, 11} = 1.16$, $P = 0.27$) did the depth of dives differ between chick-provisioning bouts in the morning and afternoon (Figure 4.5).

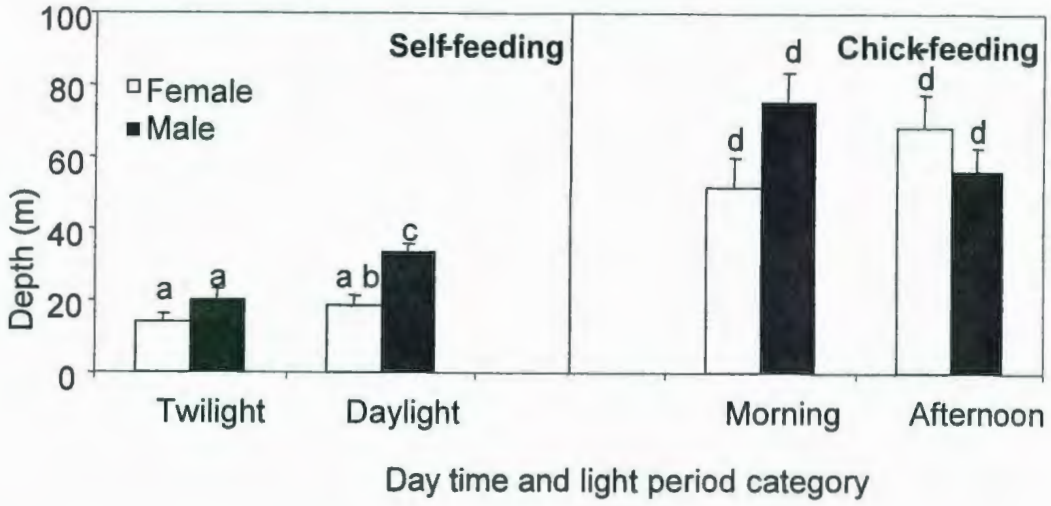

Figure 4.5 Depth dives (mean ± S.E) of male and female thick-billed murre's self-feeding and chick provisioning bouts according to day time periods ("morning": females = 03:30 h-09:30 h, N = 9; males: 05:31 h-09:30 h, N = 3 and "afternoon": females: 13:30 h-19:30 h, N = 4, males: 11:30 h-19:30 h, N = 13) and light periods ("twilight":03:30 h-05:30 h and 19:31 h-21:30 h, and "daylight": 05:31 h-19:30 h). Different letters above bars denote statistiscal differences between (ANOVA: P = 0.003) and within sexes (*t*-test, P = 0.018). For example, dive depth at twilight was significantly shallower than at daylight for males but not for females.

Females had most of their self-feeding diving bouts during "self-feeding only" trips (91%, N =310), while about half of males' self-feeding diving bouts occurred during provisioning trips (49%, N = 411, Figure 4.6). Within "self-feeding only" trips, females had significantly more bouts than males during the last trip of the day ("no return to colony, overnight at sea"; Chi-square test: χ^2_1= 165.6, P < 0.001) Males had significantly more self-feeding bouts during provisioning trips (Chi-square test: χ^2_1= 207.24, P <

0.001) and in between provisioning trips ("return to colony", Chi-square test: χ^2_1= 15.208, $P < 0.025$) than females.

Figure 4.6 Proportion of self-feeding bouts of male and female thick-billed murre according to provisioning trips and "self-feeding only" trips. The latter includes two sub-categories: trips with return to colony without meal delivery ("return to colony") and trips after last provisioning at the end of the day (" no return" overnight at sea). Asterix (*) denotes statitistical differences between sexes (Chi-Square test, $P < 0.05$).

4.4.2 Foraging trips and time spent from foraging areas

I examined whether males and females had similar foraging trip durations and flight times from the foraging to the breeding site and if the sexes behaved differently as a function of whether or not the trip was for chick provisioning. There was significant interaction between sex and type of trip duration ($F_{1, 37} = 10.37$, $P = 0.003$), so we

analyzed the main factors independently. Females had similar duration foraging trips regardless of whether they brought food to their chicks (squared-root transformed data, ANOVA: $F_{1, 21} = 0.08$, $P = 0.78$; Figure 4.7 a). In contrast, males had longer foraging trip durations when they delivered food to their chick than when they did not (ANOVA: $F_{1, 17} = 17.33$, $P = 0.001$). Males had longer foraging trip durations than females only when they brought food to their chicks (ANOVA: $F_{1, 21} = 38.63$, $P < 0.0005$); the sexes did not differ in foraging trip duration when no meal was deliverred (ANOVA: $F_{1, 17} = 2.28$, $P = 0.15$, Figure 4.7 a).

In the analysis of travel time from last dive to the breeding site (return time), I found significant interaction between sex and type of trip on the return time ($F_{1, 33} = 6.26$, $P = 0.017$). Further analysis showed that the return time of males (square-root transformed data: ANOVA: $F_{1, 16} = 3.68$, $P = 0.074$) and females (ANOVA: $F_{1, 19} = 2.28$, $P = 0.15$, Figure 4.7 b) did not differ whether or not they brought food for their chicks. However, males spent significantly longer time returning from their foraging areas when they brought food than females (ANOVA: $F_{1, 18} = 9.47$, $P = 0.007$). Returning time to the colony did not differ between sexes when there was no meal delivery (ANOVA: $F_{1, 17} = 0.44$, $P = 0.52$, Figure 4.7 b).

Figure 4.7 Foraging trips (mean ± S.E) with and without meal delivery of male ($N = 12$) and female ($N = 11$) thick-billed murres: A) trip duration, B) return time since the last dive and approximate distance. Significant differences between sexes were found only during trips with meal delivery in both analysis (*ANOVAs: $P < 0.007$); and only in trip duration in pooled data (*ANOVA: $P < 0.0005$). Within sexes, males had significant differences in duration only between trips categories (*ANOVAs: $P < 0.007$); females trip duration and return time did not differ between trip categories (ANOVAs: $P > 0.05$).

Analysis of the time-activity budget showed that males and females spent similar percentages of time at the three different activities during foraging trips for chick provisioning (Chi-square test: $\chi^2_1 = 3.203$, $P = 0.202$, Figure 4.8). Males spent longer time "flying from / to the colony" (Student t-test: $t_{1, 17} = 4.60$, $P < 0.0005$), "underwater" (Student t-test: $t_{1, 17} = 5.53$, $P < 0.0005$) and "at sea" (Student *t*-test: $t_{1, 17} = -4.28$, $P = 0.001$; Figure 4.8).

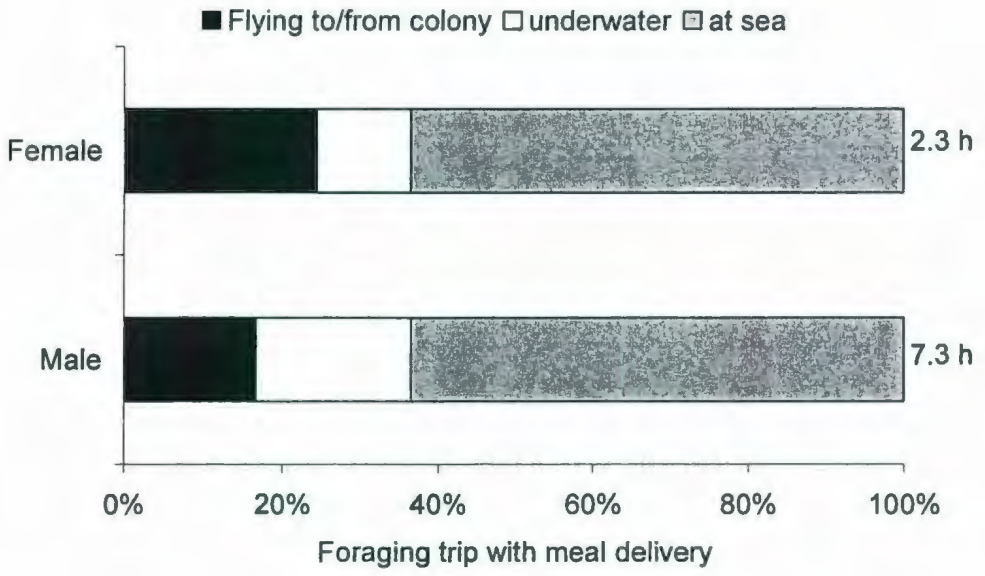

Figure 4.8. Time-activity budget of male ($N = 8$) and female ($N = 11$) thick-billed murres during chick provisioning trips at Gannet Islands, Labrador.

4.4.3 Prey species delivered to chicks

Parents delivered mainly daubed shanny (74%, $N = 19$) and in less proportion capelin (21 %) and eelpout (*Lycodes sp.* 5%) to their chicks. Among 11 prey items delivered by females ($N = 8$) eight were daubed shannies (2 females duplicated) and three were capelin (one female duplicated). Of eight prey items delivered by males ($N = 6$), six were daubed shannies (one male duplicated), one capelin and one eelpout (one male delivered both species). On average, the maximum depth of dives for capturing daubed shannies and capelin were 73.2 ± 4.28 m and 74.2 ± 5.14 m respectively. The maximum depth of the only dive performed for capturing eelpout was 54 m. Males (79.0 ± 6.02 m) and females (68.9 ± 5.8 m) did not differ on their maximum depth dives for capturing daubed shanny (Student *t*-test: $t_{1, 12} = 1.22$, $P = 0.25$). The maximum depth for capturing capelin was 70.57 ± 5.18 m for females, and 85 m for a one male.

4.5 DISCUSSION

4.5.1 Effect of time-depth recorders in birds' behaviour

In a previous study (Paredes *et al.* 2005), I have shown that attached data loggers affect thick-billed murres' body mass and parental behaviour. Because murre males and females are monomorphic and were treated equally in our procedures, I assumed any effect of TDRs on the behaviour of our birds would have been the same for all birds. Thus, differences in behaviour should have been a result of their foraging strategies not spurious instrumentation effects. For instance, sex differences in foraging trip duration occurred naturally in non-equipped murres; males have longer trips than females (Paredes *et al.* 2006). By flying to further foraging areas (see below) males might experience higher energy expenditure than females and be reflected in their body condition. TDR-equipped males lost weight at a higher rate than TDR-equipped females (Paredes *et al.* 2005). Both these results indicate a strong effect of instrumentation on murres' flying performance as expected by their high-wing loading characteristics.

Peaks of chick provisioning dives coincided with peaks of prey delivery of non-TDR equipped male (mid-day and early afternoon) and female (early morning/ late afternoon) murres at the Gannet Islands, Labrador (Paredes *et al.* 2006). However, instrumented females had a higher delivery rates in the morning than in the afternoon,

which also concur with a previous study of diving behaviour of murres at Gannet Islands (Jones *et al.* 2002). Females, especially those with the extra work of carrying TDRs, might be in better condition at the beginning of the day because they had time for replenishing energy reserves during periods of prey abundance at twilight before engaging in chick provisioning.

4.5.2 Chick-provisioning foraging

In seabird species, the parent that provides more meals to their chicks shows a characteristic foraging behaviour. For instance, they travel to closer foraging areas, dive shallower and provide larger or more energy rich prey than their mates (Weimerskirch *et al.* 1997; Gray & Hamer 2001; Kato *et al.* 2000; Clarke 2001). In thick-billed murres, I found that they dived deeper for chick provisioning than for self-feeding irrespective of the sex or the time of day. In addition, sexes did not differ in the number of dives per bout nor in other dive parameters (duration, bottom time, and descent and ascent rates). Both these results suggest that the sexes do not differ in the allocation of effort for chick-provisioning diving. Both parents feed their chicks mainly with benthic preys (i.e. daubed shanny; Bryant & Jones 1999; Chapter 3) although other prey items such as small crustaceans are a considerable component of adult murre's diet year around (Gaston & Jones 1998; Melhum 1996, 2001). In fact, incubating murres dived shallower than chick-rearing murres, which probably reflected capturing crustaceans versus fish (Benvenutti *et*

al. 2000). Thus, deep diving may allow murres to provide larger or better preys to their chicks although probably at a higher cost.

Both sexes performed fewer dives during chick-provisioning bouts than self-feeding bouts. This suggest that murres are likely to seek ideal foraging areas when they search for their chick's food, so costs related to deep diving are minimized. In fact, murres are able to locate "hot spots" of food during reproduction (Cairns & Schneider 1990; Davoren *et al.* 2003) and have strong fidelity to their foraging areas at spatial scales of 1-20 km in Kongsfjorden (79° N; Mehlum *et al.* 2001).

Previous studies have shown that on average female chick-rearing thick-billed murres have shorter foraging trips than males at Gannet Islands (Paredes *et al.* 2005, 2006). We found that females had shorter trips and return time to the colony than males when they were foraging for chick provisioning but not for self-feeding. Although sex and type of foraging trip was not distinguished, there is evidence of individual tendency to perform short or long foraging flights to reach feeding areas in thick-billed murres at Latrabjarg, Iceland (65°30' N, Benvenuti *et al.* 1998). Differences in foraging trip duration of high-arctic murres in Greenland were mostly attributed to the time spent flying to feeding areas instead of diving activity at location (Falk *et al.* 2000). Assuming thick-billed murres have a direct flight back to the colony after the last dive (Benvenuti *et al.* 1998), the average maximum distance estimated for females (32 Km) was about half of that of males, which indicate a spatial segregation of foraging areas when feeding for provisioning . Jones *et al.* (2002) did nor find sex differences on return time to the colony at Gannet Islands, which may be explained by the use of radio-transmitters instead of

direct observations of meal delivery (this study) and the assumption that all return trips ended in chick-provisioning. In fact, we did not find differences when all return trips were included. According to central place theory, foragers are expected to increase the quantity and quality (larger size for single loaders) of the prey item delivered to chicks when increased foraging distance (Orians & Pearson 1979). Although males seem to fly to more distant foraging areas than females, the sexes did not differ in the length of prey items delivered to chicks (Paredes *et al.* 2006). This may be the result of balancing costs of carrying a heavier load and flying for a long period of time by a high-wing loading species.

If both parents are diving equally deep for chick provisioning the most pressing question is why is there partitioning of foraging times and feeding areas between males and females during reproduction? Foraging for chick provisioning includes traveling, searching and capturing prey for both self-maintenance and chick meal delivery. According to provisioning models (Ydenberg 1994; Ydenberg *et al.* 1994) parents must reserve time and energy for enough self-feeding to balance their own energy budget, while maximizing their daily food delivery to offspring. Female murres forage at times when zooplancton (e.g., crustaceans) is most available in surface waters at Gannet Islands (Jones *et al.* 2002, Paredes et al. in prep.). Swarms of crustaceans move upward at dusk for feeding, and migrate downward as anti-predatory defence against visual predators at dawn (Loose & Dawidowicz 1994). One possible explanation is that by traveling to nearer foraging areas and foraging at times of prey abundance, female murres may gain energy at a faster rate for self-maintenance and therefore be able to provision offspring at

a higher rate. Whether similar distinctive foraging strategies occur in other auk females (Wanless & Harris 1986; Creelman & Storey 1991; Fraser *et al.* 2002; Wilhem 2004; Paredes et al. 2006) or males (Bradley et al. 2002; Harding et al. 2004) that are mainly in charge of chick provisioning require further investigation.

Altogether these results indicate that differential foraging strategies of male and female thick-billed murres were driven by constraints associated to parental care (i.e. chick nutritional needs) and self-feeding foraging was adopted accordingly.

4.5.2 Self-feeding foraging

During self-feeding individuals capture and ingest food for their own maintenance instead of sharing or storing it for later delivery as occurs for chick-feeding. In theory, murres could adopt two different strategies for self-feeding foraging, "rate maximizing" (gain/time) and efficiency maximizing" (gain/expenditure), according to their requirements and environmental pressures (Ydenberg *et al.*1994). At Gannet Islands, murres seem to fill their requirements for self-maintenance in two different ways. Most self-feeding bouts of females occurred during "self-feeding only" trips (91%), which occur mainly at the end of the day (68%, before sunset). Because females usually remained at sea overnight, they were able to feed exclusively for self-maintenance well after their last chick provisioning and before their first delivery of the new day. Thus, the main self-feeding by females, characterized by shallow diving behaviour, coincided with the vertical migration of zooplancton at dawn and dusk. Although we were unable to

determine whether females were in fact feeding on different prey for self-feeding, there is indirect evidence that suggests crustaceans are an important component of the diet of adults at Gannet Islands (Jones *et al.* 2002; Chapter 3). By foraging in swarms of crustaceans during twilight periods female murres may be reducing energy expenditure costs by intense foraging. Thus, most female self-feeding foraging appears to fit the rate maximizing strategy because although food is abundant its availability is constrained by time.

Self-feeding foraging in male murres occurred during (49%) and in between chick provisioning trips (31%). During provisioning trips, sexes did not differ on depth and other dive parameters when feeding for self-maintenance suggesting they were feeding on similar preys than those delivered to their chicks. At Gannet Islands, male murres delivered significantly more capelin than females (Chapter 3); this fish can be found at different levels of the water column during the reproductive season (Montevechhi & Piatt 1984). In contrast, male murres dived deeper and have faster ascent rates than female murres during self-feeding-only trips, which suggest they were seeking different prey. Efficient divers are expected to adjust their behaviour underwater to maximize feeding time over the dive cycle (Kramer 1988, Houston and Carbone1992, Mori *et al.* 2002). Despite the differences in dive depth, males spent similar time at the bottom (i.e. capturing/ingesting prey) and descend at similar rates than females. Murres are able to adjust their angle (Wilson *et al.* 1996, Ropert-Coudert *et al.* 2001, Sato *et al.* 2003) or/and swimming speed accordingly to the behaviour of their preys (Lovvorn *et al.* 1999, 2004). Thus, males may be descending at sharper angles than females so they can reach

deeper depths at similar rates. In fact, U-shaped dives characterized diving profiles of murre males while W-shaped dives characterized female profiles at Gannet islands (Chapter 3). The shorter "self-feeding only" trips and the return time to the colony suggest that males might be flying to closer feeding areas when foraging exclusively for self-feeding. Thus, males foraging strategy for self-feeding seems to be more oportunistic than that of females. Although, both sexes distributed their time similarly among activities at sea, the amount of time males spent underwater, flying from or to feeding areas, and resting at sea was significantly more than for females. Greater resting time at the surface may allow males to digest food and recover from costs incurred during the first part of the foraging trip ("digestive strategy", Sibly 1981; see also Jackson 1992). Thus, male's self-feeding behaviour seemed not to be constrained by time but by energy costs of deep diving and flying to further feeding areas during provisioning trips, so lower feeding rates were expected. By balancing their total energy budget, males might be maximizing their total daily gain and delivery rate, which is similar to an efficiency maximizing strategy.

Interestingly, bottom time and descent rate did not differ between the sexes despite their differences in depth during self-feeding dives. Diving-flying birds are not only limited by a limited oxigen supply, and changes in presure depths, but also by the need to carry large oxigen supplies that aid to reduce flying costs (Lovvorn & Jones 1994). As a result, they experienced an increased bouyancy underwater and therefore increased diving costs (Wilson *et al.* 1992b). Work against bouyancy become minimal below the depth at which most compression of air spaces has occurred (~20 m; Lovvorn & Jones 1991; Lovvorn,

2001), and much of the energy expended against buoyancy during descent may be recovered during ascent (i.e. gliding effect, Lovvorn *et al.* 1999). Their narrow depth range (20-32 m) exposed to negative bouyancy, might explain similar descent rates of male and female thick-billed murres during self-feeding. Faster ascent rates of males migth be needed to minimize oxygen depletion and maximize capturing/ingesting time at the bottom.

In summary, male and female thick-billed murres at the Gannet Islands, Labrador seemed to use different foraging areas, but decended to similar depths and captured similar prey for chick provisioning suggesting similar effort allocation underwater. On the other hand, they dived to different depths to capture what was available for self-feeding at the respective time of day each sex foraged. Taken together, these results suggest different strategies of males and females for self-feeding and chick-provisioning foraging, reflecting different energy and time constraints, which seem to be associated with their parental roles.

4.6 ACKNOWLEDGMENTS

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CHAPTER 5: SEX DIFFERENCES IN AGGRESSIVE BEHAVIOUR IN THICK-BILLED MURRES AND RAZORBILLS

5.1 ABSTRACT

Parental aggression in the form of offspring defence directly affects offspring survival and consequently the adult's fitness. Seabirds tend to be sexually monomorphic with biparental care of their young and as a result sex differences in parental aggression are not expected. The four species in the Alcini tribe, however, have an intermediate form of parental care - biparental at the breeding site followed by male-only at sea – and therefore may have evolved sex biases in parental aggression. Here, I set out to measure sexual dimorphism and to test for sex bias in parental aggression in two sympatric Alcini species, razorbills, *Alca torda*, and thick-billed murres, *Uria lomvia*. I made morphological measurements and studied aggression levels of attending male and female thick-billed murres and razorbills during the incubation and brooding period in 2002 at the Gannet Islands, Labrador. I found that males were significantly larger than females in culmen and gape length in both species. Murres were also sexually dimorphic in body mass. I measured parental aggression in two ways: frequencies of aggressive interactions and, in razorbills only, the response to the presentations of a predator-model. I found that during the incubation period, thick-billed murre males initiated most of the aggressive

interactions (78% vs. 58%). During the brooding period, razorbill males responded aggressively to intruders more frequently than females (98% vs. 89%). Although the level of conspecific aggressive behaviour was not different among sexes in both species, male razorbills performed most of the high-scored aggressive responses such as chasing and fighting (64%). In response to presentations of the predator model, male razorbills responded aggressively more often (88% vs. 41%) and more intensely than females. Overall, my results indicate a male-bias in parental aggressive behaviour in murres and razorbills. Whether by cause or effect, elevated male parental aggression maybe directly related to male-only accompaniment of chicks at sea.

5.2 INTRODUCTION

Parental aggression in the form of defence or protection of their offspring increases the parent's fitness by reducing the likelihood of offspring mortality. However, there are costs in terms of risk, energy and time for the parent that shows such aggressive behaviour during reproduction. In theory, optimal intensity of nest defence should maximize net fitness benefits of the aggressive parent (Montgomerie & Weatherhead 1988). Parental or defensive aggression may be shown by one or both sexes; which largely depend on their forms of parental care and mating systems. In the majority of insects, fish and many mammal species, only one parent takes care of the egg or offspring

(Clutton-Brock 1991; Crawford & Balon 1996; Trumbo 1996). Consequently, defence decisions by the caregiver are relatively simple. In the majority of monogamous bird species both parents share parental duties, however there is often specialization in defensive aggression by one sex (review by Archer 1988). Male-biased aggressive behaviour reported in some penguins (Spurr 1974; Moreno *et al.* 1995), gulls (Morris & Bidochka 1982; Butler & Janes-Butler 1983) and passerines with facultative mating systems (i.e. polygyny: Knight & Temple 1988) has been attributed to territorial and mate defence because it occurs only or more intensively during the courtship and laying period.

In contrast, in many of the bird species that practice biparental care, males play major roles in nest defence and this persists throughout the chick-rearing period (passerines: Regelmann & Curio 1986; Breitwisch 1988; Lombardo 1991; Winkler 1992; Hogstad 2005; eastern screech owl, *Otus asio*, Sproat & Ritchison 1993; Northern lapwing, *Vanellus vanellus*, Kis *et al.* 2000; gulls, *Larus spp.*, Pierotti 1981; Southern 1981; black skimmer, *Rhynchops niger*, Burger 1981; and Atlantic puffin, *Fratercula arctica*, Creelman & Storey 1980). Sex differences in aggressive behaviour have been attributed to differential capacity of defending the offspring (size or manoeurability: Pierotti 1981; Sproat & Ritchison 1993; Kis *et al.* 2000), body condition (Hogstad 2005), and sex-biased populations (Breitwisch 1988).

The Alcini tribe, composed of thick-billed murres, *Uria lomvia*, common murres, *Uria aalge*, razorbills, *Alca torda* and little auks, *Alle alle*, is an interesting group for

investigating sex differences in parental roles. Although they are not overtly sexually dimorphic seabirds, slight differences in some morphological measurements have been reported for all of these species (see reviews by Gaston & Jones 1998; Gaston & Hipfner 2000; Ainley *et al.* 2002; Hipfner & Chapdelaine 2002). In these species, both parents take care of a single offspring at the breeding site for 2-4 weeks, and it is only the male that takes care of the partially grown chick for the subsequent 3-4 weeks at sea (Gaston & Jones 1998; Stempniewicz 1995; Harding *et al.* 2004). There are several proposed explanations for the "intermediate" chick development and departure strategy shown by the four Alcini species (Cody 1971; Houston *et al.* 1996; Gaston & Jones 1998; Ydenberg 1989). However, there is no evolutionary, behavioural or ecological explanation for why males are the selected sex to accompany the chick at sea. According to Birkhead (1985), the off-duty murre parent generally defends the breeding site, while the on-duty parent avoids such aggressive interactions. Previous studies at the Gannet Islands have shown that in both thick-billed murres and razorbills males spend more off-duty time at the breeding site, suggesting its greater involvement in the defence of egg/chick, breeding site and mate than females (Paredes *et al.* 2006).

In this study, I set out to measure sexual size dimorphism and to test for sex bias in parental aggression in two sympatric Alcini species, razorbills and thick-billed murres. I studied the aggressive behaviour of the on-duty parent in the absence of its mate in order to ensure that the aggression was directed toward the protection of the egg/offspring instead of the mate. I measured aggressive responses of attending

individuals (egg/chick) in two different conditions: a) opportunistic observations of aggressive interactions between con- and heterospecifics; and b) experimental observations of aggressive behaviour resulting from the presentation of a model predator. My results address the functionality of parental or defensive aggression and the selective pressures and constraints that shape differences between the sexes.

5.3 METHODS

The study was undertaken at a mixed colony of thick-billed murres and razorbills located at GC4, one of the six islets of the Gannet Islands, Labrador (53°56′N, 56°32′W) during June-August 2001 and 2002. Murres were observed for 21 days (378 h) during their incubation period only in 2001. Razorbills were observed during 30 days (540 h) of the incubation period and 12 days (192 h) of the brooding period in 2002. The focal murres (29 pairs) were part of a colony (ca. 150 pairs) located on the top-most cliff ledge in the breeding area known as "Grey Cup"; three common murre pairs were also located in the same study area among the focal thick-billed murres. The razorbill group (31 pairs) was located on the mid and bottom part of the same cliff used by murres, and was part of a colony of open and crevice breeding sites on the cliff (approx. 45 pairs) and beach area (approx. 60 pairs) respectively.

Other species using the same breeding area (Grey Cup) were black-legged kittiwakes (4-5 pairs; *Rissa tridactyla*) and Atlantic puffins. The principal predator for chicks and to a lesser degree for adults was the great black-backed gull, *Larus marinus*; a total of 25 pairs nest on the Gannet Islands (Robertson & Elliot 2002). Other occasional predators observed include peregrine falcons, *Falco peregrinus*, northern ravens, *Corvus coræx*, and herring gulls, *Larus argentatus*.

I collected two types of data to compare levels of aggressive behaviour between males and females: a) frequency of aggressive interactions of attending birds during the incubation and brooding period and b) responses of brooding razorbills to the presentation of a model predator.

5.3.1 Aggressive interactions

During the incubation period, opportunistic aggressive interaction data were recorded continuously, concurrent with breeding site attendance observations (04:00–23:00). This was feasible because in comparison to the brooding period other parental activities were less frequent (i.e. shifts.) or absent (i.e. feedings). During the brooding period, it was necessary to conduct the same observations during two four-hour focal blocks each day (04:00–08:00, 08:00–12:00, 12:00–16:00, and 16:00–20:00) so that a full day observation was completed every two days. Observations of aggressive interactions of brooding murres were not possible because of other research activities happening at the time chicks were hatched (i.e. lack of assistants).

In murres, I recorded 178 aggressive interactions (females = 104 and males= 74) in which incubating birds either initiated or responded to an attack from an intruder. I recorded 672 aggressive interactions of attending razorbills during the incubation period (females = 340, males = 332) and 171 interactions during the chick-rearing period (females = 68, males= 103).

Observations were made from a blind, using a 20 - 60 X, 60 mm zoom spotting scope and10 x 50 mm binoculars. During each session, I recorded all aggressive interactions of marked subjects attending either eggs or chicks. I focused my observations on birds that were either incubating or brooding rather than off-duty parents because they were more likely to be defending the offspring compared to the territory, breeding site or mate. During each interaction, I recorded the ID of the breeding site owner (note that sex was not known at this point), breeding site condition (egg/chick), intruder species and its distance to the breeding site owner, initiator of the aggression, and the aggressive behaviour of the breeding site owner.

Thick-billed murres breed in denser colonies than razorbills so the likelihood and direction of aggressive interactions between the breeding site owner and neighbours or intruders was different. Murre breeding site owners were physically in contact with 1– 4 neighbours at the same time. In contrast, razorbills were generally ca. 1 m from their nearest neighbour and so body contact was unusual. As a result, murre breeding site owners would initiate or respond to attacks from neighbours (attending, arriving, and departing) or intruders (con- or heterospecifics); attending razorbills would mostly initiate attacks on intruders present near their breeding site.

The distance between the breeding site owner and the intruder was estimated from the observation blind using the maximum width of a razorbill's body (0.15 m) as a reference. I recorded six forms of aggressive display in murres: a) head movement toward intruder without contact, b) vocalization, c) pecking without leaving the nest, d) standing and looking at the intruder without leaving the nest, e) chasing (bird leaves the nest to follow intruder), and i) fight (includes pecks, bites, wing strikes, rolling on the ground and sometimes falling down the cliffs). I recorded nine aggressive displays in razorbills: a) open bill, b) bill flapping, c) head shaking, d) head movement toward intruder without contact, e) vocalization f), pecking without leaving the nest, g) standing and looking at the intruder without leaving the nest, h) chasing (bird leaves the nest to follow intruder), and i) fight (includes pecks, bites, wing strikes, rolling on the ground and sometimes falling down the cliffs). I also recorded whether there was no response or a negative response such as a) movement away from the intruder but remaining near egg/chick, b) temporary abandonment of the breeding site. Ordinal scores were assigned according to the subjectively judged degree of aggression. Murre behavioural responses were scored as follows: 0 = no response; 1 = move toward intruder and vocalization (no contact); 2 = pecking ($\geq$1; on breeding site); 3 = standing at the level of intruder and chasing; and 4 = fight. Razorbill responses were scored as follows: -2 = breeding site abandonment; -1 = move away from breeding site; 0 = no response; 1 = bill open, bill flapping, and head shaking (on breeding site); 2 = head movement towards intruder, and vocalization (no contact); 3 = pecking ($\geq$ 1; on breeding site); 4 = standing at the level of intruder and

chasing, and 5 = fight. The scores of the same individual were averaged before the analysis to account for possible replication.

Individuals were identified by temporary marks of picric acid (yellow) or fluorescent paint (green, pink and orange) delivered from a small open-top container (10 ml of the marking liquid) attached to the tip of a 4 m graphite pole. This method allowed marking from above the birds without disturbing the colony. Individual mark patterns along with other life history information were recorded on ID cards for quick reference. One member of each pair was captured during the chick-rearing period for permanent marking (i.e. banding), morphological measurements and sex determination. Twenty-six additional birds were captured from other areas in order to supplement the between-sex comparison dataset.

Murres were captured with a noose of nylon monofilament (1.5 mm diameter) on the end of a 4-m graphite pole. Razorbills were captured with a small weighted noose-carpet (ca. 15-30 short slip-knots of monofilament line attached to a 0.3 x 0.2 m wire carpet laid on the ground) or noose string (ca. 10-20 short monofilament slip knots attached to a 0.3 - 0.4 m single main line) attached to 20 m of nylon monofilament line (1.5 mm diameter) with the other end attached to a 3 m wooden pole. The carpet or string was positioned on cliff ledges used by the birds; birds would become entangled by the legs and feet as they approached or departed their breeding site.

Once captured, birds were permanently marked with a field readable stainless steel leg band and a color band. Weights were taken with a Pesola balance to the nearest

5 g, and wing cord and tail length (tail-tip to where feathers join the skin under the uropygial gland) were measured with a steel ruler to the nearest 1 mm. Measurements of the culmen (bill-tip to where feathers meet the top of the bill), bill depth at gonys, and gape length (bill-tip to where mandibles join) used vernier callipers accurate to the nearest 0.1 mm. Blood samples (0.5 ml) were taken from the tarsal vein and stored in 95% ethanol for later sex determination using molecular DNA analysis (Fridolfsson & Ellegren 1999). In addition, six razorbills were sexed by behavioural observations; males were seen leaving the colony with the chick. The results of sexing were obtained after the season was finished (during the fieldwork observers were did not know the sex of birds) and then matched with the ID cards to interpret behavioural data.

5.3.2 Model presentation

I presented a model predator, a stuffed great black-backed gull, to 17 pairs of brooding razorbills with chicks 9-12 days old. The dead gull was donated by the Canadian Wildlife Service, NL and taxidermy was done by RP at Memorial University. The model was attached to a 2 m-wooden pole and presented on the ground with wings folded as if it were walking toward the breeding site. The model was presented from a hidden site to each sex of a breeding pair when the mates were absent. During each session, the model was presented first at 3 m distance for 3 minutes, and then moved to a second position, 1 m away from the breeding site for another 3 minutes. I scored the model trials using the

same methods and metrics used to score the observations of aggressive interactions (detailed above). Additional behavioural responses observed and recorded during the model trials included protective behaviour: a) move toward the chick, and b) accommodate the chick under the wings.

5.3.3 Statistical analysis

Statistical analyses used SPSS version 11.5. I used parametric tests (Student *t*-test for independent samples, and paired *t*-test) to compare groups if the residuals met the assumptions for the general linear model and non-parametric tests when they did not. There was the possibility of Type II error when hypothesis null of rank-based tests was accepted. Chi-Square test and Fishers' exact test was used to compare proportions when sample sizes were large and small respectively. Means are expressed ± SE. All comparisons were two-tailed and differences were considered significant when $P < 0.05$.

5.4 RESULTS

5.4.1 Morphological measurements

In both species, sexes differed significantly in some bill dimensions; males had longer gape and culmen than females (Table 5.1 & 5.2). Male thick-billed murres were significantly heavier than females (Table 5.1). Male razorbill had greater depth bill than females (Table 5.2). There were not sex differences in wing cord, tail length in both species (Table 5.1 & 5.2).

Table 5.1 Measurements of male ($N = 29$) and female ($N = 35$) thick-billed murres captured at the Gannet Islands Labrador during the 2000-2002 breeding seasons.

	Female			Male			*t*	*P*
	Mean	SD	N	Mean	SD	N		
Body mass (g)	905.77	58.47	44	949.21	70.11	39	-3.073	0.003
Culmen (mm)	33.22	0.20	45	34.80	0.22	39	-3.443	0.001
Bill depth (mm)	13.95	0.01	45	14.21	0.05	39	-1.507	0.136
Gape (mm)	58.90	0.32	45	60.92	0.35	39	-2.723	0.008
Wing cord (mm)	211.2	0.54	45	212.7	0.57	38	-1.193	0.236
Tail length (mm)	64.0	0.53	43	64.7	0.59	34	-0.609	0.544

t = t-tests for independent samples (two-tailed).

Table 5.2 Measurements of male ($N = 26$) and female ($N = 26$) razorbills captured at the Gannet Islands, Labrador during the 2000-2003 breeding seasons.

	Female			Male			*t*	*P*
	Mean	SD	N	Mean	SD	N		
Body mass (g)	705	43.9	27	705	37.6	29	0.046	0.963
Culmen (mm)	32.9	0.10	26	33.9	0.15	26	-2.760	0.008
Bill depth (mm)	22.8	0.06	26	23.3	0.07	26	-2.551	0.014
Gape (mm)	52.2	0.29	26	54.0	0.22	26	-2.552	0.014
Wing cord (mm)	205	20.45	26	205	0.63	26	0.562	0.576

t = t-tests for independent samples (two-tailed).

5.4.2 Thick-billed murres

Most of the aggressive interactions occurred between conspecifics (90%, $N = 162$). The majority of heterospecific interactions (94%, $N = 16$) involved neighbouring common murres. About 46% of the aggressive interactions ($N = 162$) occurred between neighbours and 54% between unknown adults. Numerically, females ($N = 104$) had more aggressive interactions than males ($N = 74$). However, aggression was more often initiated by males (80%, $N = 74$ interactions); females were attacked by conspecifics and heterospecifics more often than males (42%, $N = 104$ interactions; Chi-square test: $\chi^2_1 = 6.888$, $P = 0.009$). Attacks were nearly always responded to (males: 99.4%, $N = 14$; females: 99%, N

= 41) with no sex difference. The same results were found when only conspecific interactions were analyzed; males initiated most of the aggressive interactions and females mostly received attacks from con-specifics (Chi-square test: $\chi^2_1 = 5.529$, $P = 0.019$; Figure 5.1).

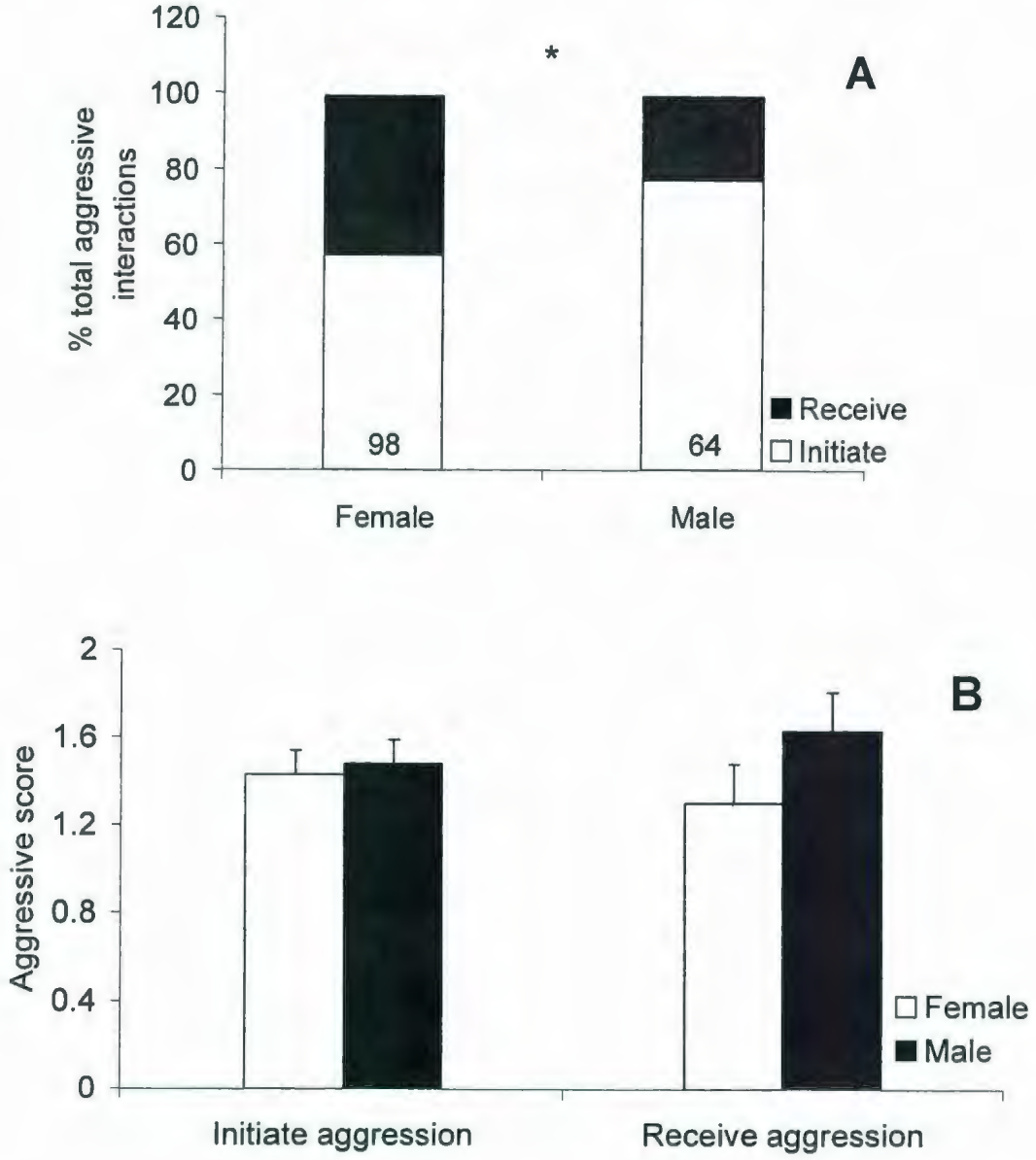

Figure 5.1 Frequency of aggressive interactions (A) and scores (B) of female and male thick-billed murres according to whether the adult initiate the aggression ("initiate") or respond and attack ("receive") from a conspecific during the incubation period. Means ± SE are shown.

Results of the aggression intensity scores for all incubating murre interactions showed no significant differences between males (1.56 ± 0.09; $N = 31$) and females (1.47 ± 0.11, $N = 44$; Mann-Whitney U test: $U = 553.0$, $P = 0.073$). The same results held true when only conspecific interactions were analyzed (males: 1.52 ± 0.09, $N = 26$; females: 1.43 ± 0.12, $N = 43$; Mann-Whitney U test: $U = 452.0$, $P = 0.075$). Furthermore, mean aggression scores did not differ between sexes whether the adults initiated (Mann-Whitney U test: $U = 234.0$, $P = 0.328$) or responded to attacks (Mann-Whitney U test: $U = 63.00$, $P = 0.082$; Figure 5.1). Despite the many aggressive interactions, there were few actual fights; of five fights, all were between conspecifics, four involved females responding and one involved a male initiating.

5.4.3 Razorbills

The estimated distance between the breeding site owner and the intruder varied between 0 –3 m. The average distance that produced an aggressive reaction from the incubating adult was 0.21 ± 0.01 m. In those cases where there were aggressive responses from razorbills, sexes did not differ in their average distance to the intruder during incubation (males: 0.20 ± 0.02 m, $N = 299$; females: 0.21 ± 0.02 m, $N = 302$; Student t test: $t_{1, 463} = 0.289$, $P = 0.773$) and brooding (males: 0.25 ± 0.03 m, $N = 101$; females: 0.25 ± 0.02 m, $N = 61$; Student t-test: $t_{1, 129} = -0.028$, $P = 0.978$) .

During the razorbill incubation period, there were no sex differences in frequency of aggressive responses (females: 89%, $N = 340$; males: 90%, $N = 332$; Chi-square test: $\chi^2_1 = 0.272$, $P = 0.301$). Most of the aggressive interactions involved conspecifics (91%, $N = 672$) whether it produced an aggressive response or not from the nest owner. Most of these interactions involved unknown razorbills while only few (1– 2%) involved neighbours. Most of the heterospecific interactions involved murres (69%, $N = 59$), followed by puffins (19%) and gulls (12%). The same results were found when only the conspecifics interactions were analyzed; no differences were found in the frequency of aggressive behaviour between sexes (Chi-square test: $\chi^2_1 = 0.015$, $P = 0.452$; Figure 5.2).

Results of the aggression intensity scores for all incubating razorbill interactions showed no significant differences between males (1.83 ± 0.09, $N = 38$) and females (1.76 ± 0.11, $N = 31$; Mann-Whitney U test: $U = 538.5$, $P = 0.528$). The same result held true (i.e. no sex difference in aggression intensity) for interactions involving either conspecifics (Mann-Whitney U test: $U = 203.0$, $P = 0.668$; Figure 5.2) or heterospecifics (Mann-Whitney U test: $U = 86.00$, $P = 0.942$).

During the brooding period, male razorbills responded aggressively more frequently to the presence of intruders than females (98%, $N = 103$ vs. 89%, $N = 68$; Chi-square test: $\chi^2_1 = 5.731$, $P = 0.017$). Most of the aggressive interactions involved conspecifics (87 %, $N = 171$). The remaining heterospecific interactions (13%, $N = 171$) involved mostly murres (55%) and puffins (41%). The same result held true (i.e. frequency of aggression was higher in males) when only conspecific interactions were analyzed (Chi-square test: $\chi^2_1 = 5.376$, $P = 0.020$; Figure 5.2).

Results of the aggression intensity scores for all brooding razorbill interactions showed no significant differences between males (2.43 ± 0.17, $N = 18$) and females (2.06 ± 0.13, $N = 23$,; Mann-Whitney U test: $U = 3232.0$, $P = 0.193$). The same result held true (i.e. no sex difference in aggression intensity) for interactions involving either conspecifics (Mann-Whitney U test: $U = 69.0$, $P = 0.302$; Figure 5.2) or heterospecifics (Mann-Whitney U test: $U = 19.50$, $P = 0.699$). Males performed most of the interactions with the highest aggression scores (67%, $N = 41$, 4 = stand and chase, 5 = fight). Only one fight was recorded and it was between a male razorbill and a thick-billed murre.

Over the course of a breeding season, higher aggression intensity scores were found during brooding (2.27 ± 0.11) compared to incubation (1.80 ± 0.07; Mann-Whitney U test: $U = 842.5$, $P < 0.0005$). These differences were found in both razorbill males (Mann-Whitney U test: $U = 241.5$, $P = 0.003$) and females (Mann-Whitney U test: $U = 181.5$, $P = 0.039$; Figure 5.2).

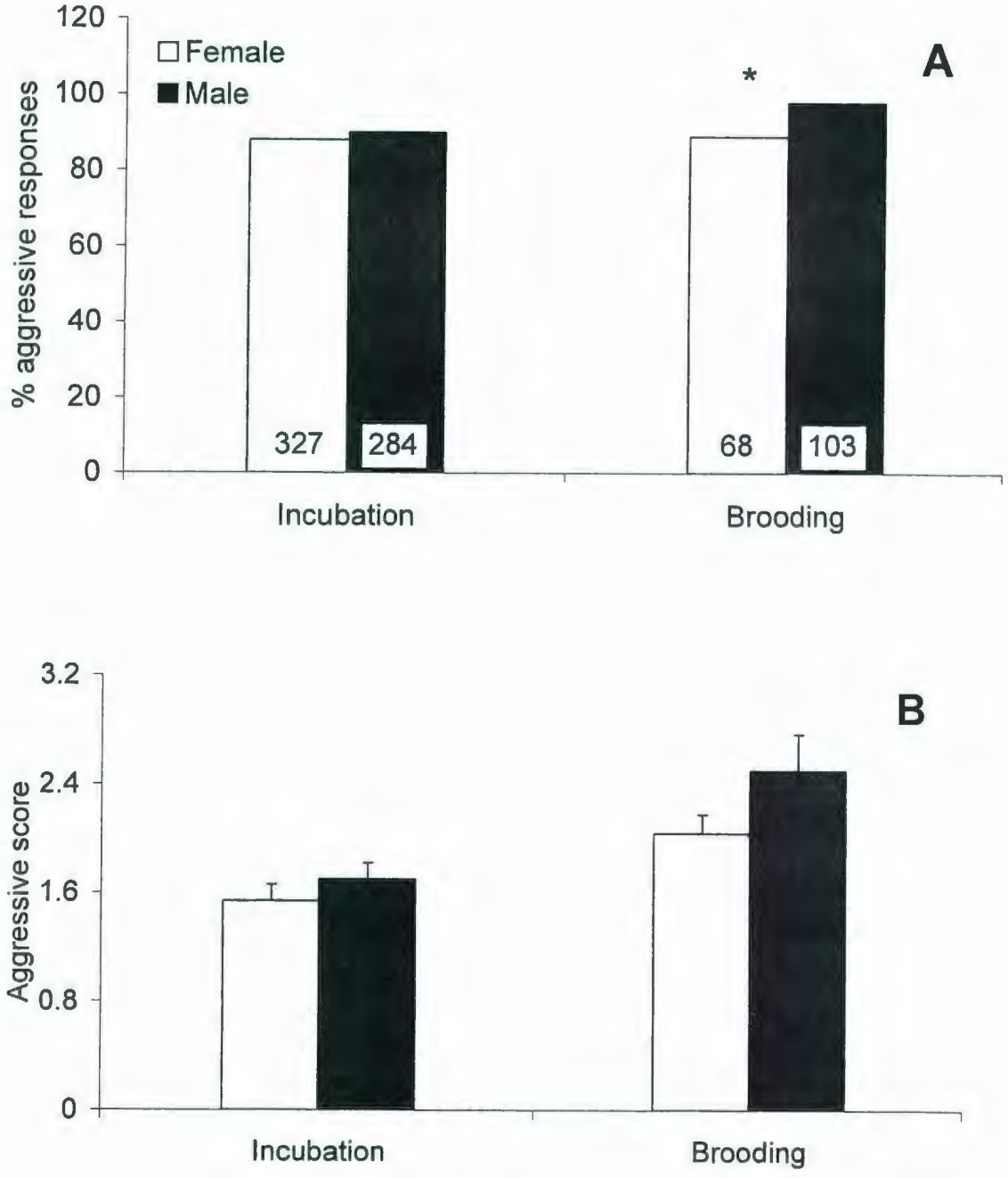

Figure 5.2 Frequency of aggressive interactions (A) and scores (B) of female and male razorbill according to whether the adult respond to the presence of a conspecific during the incubation and brooding period. Means ± SE are shown. Sample size inside bars represents the total number of interactions (responses + no responses).

5.4.4 Model Predator Presentation

The frequency and type of responses to the model predator (gull) presentation differed significantly between sexes (Figure 5.3). At both distances from which the gull model was presented, males responded with positive aggressive behaviours significantly more than females, and females responded with negative or neutral aggressive behaviours more than males (3m: Chi-square test: $\chi^2_1 = 4.371$, $P = 0.019$; 1m: Chi-square test: $\chi^2_1 = 6.585$, $P = 0.005$; Figure 5.3). Most of the cases where razorbills showed no response (78%, $N = 9$) to the predator model occurred at 3 m distance. On average, male razorbills showed higher aggression intensity scores than females at both model presentation distances (1m: Mann-Whitney U test: $U = 73.00$, $P = 0.013$; 3m: Mann-Whitney U test: $U = 82.5$, $P = 0.031$; Figure 5.4). In addition, more males than females showed protective behaviour (move toward and covered the chick) at both model presentation distances (3 m: 8 vs.1 out of 17 of each sex; $P = 0.017$, Fisher's exact test; 1 m: 7 vs. 0 out of 17 of each sex; $P = 0.003$, Fisher's exact test).

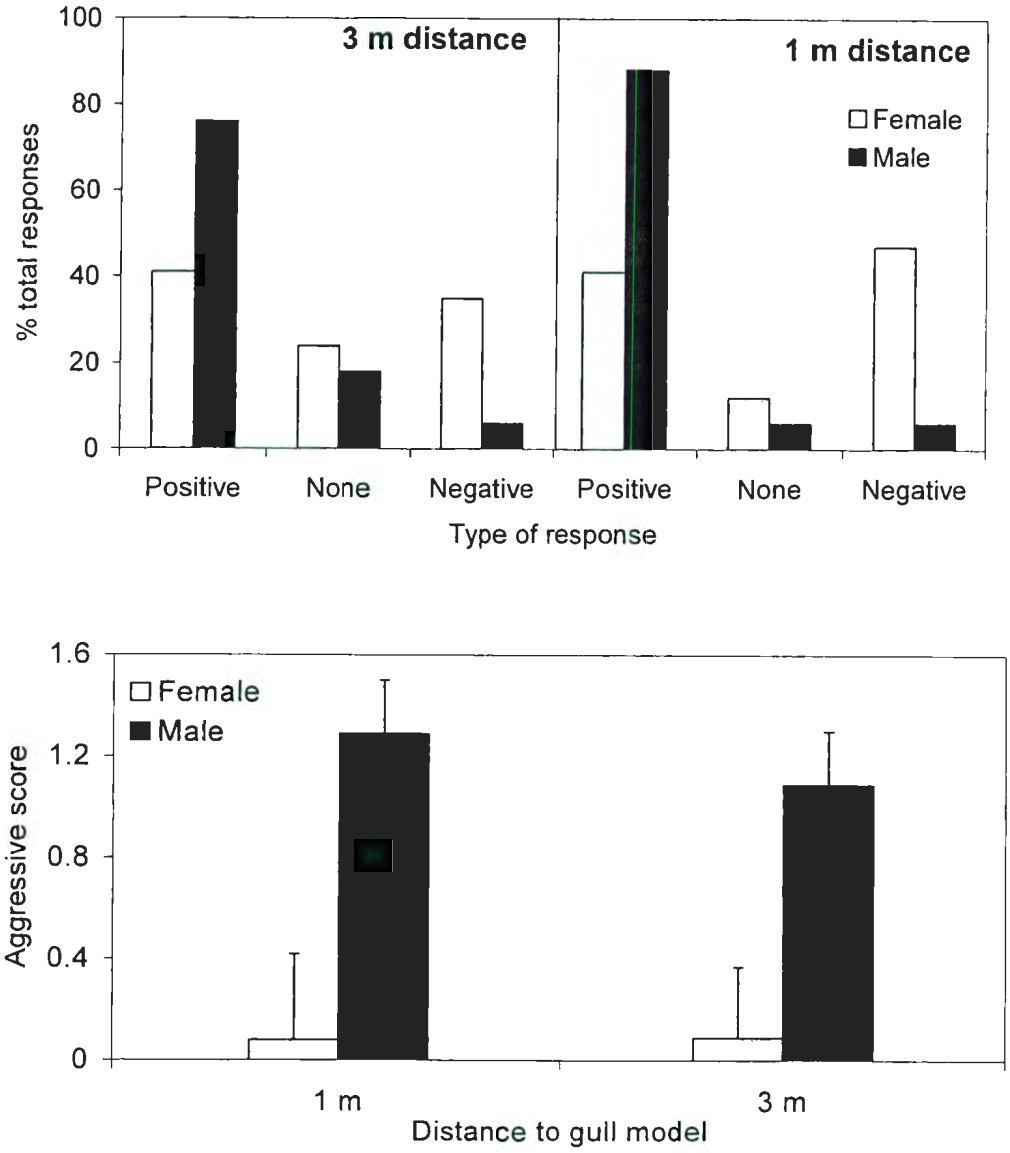

Figure 5.3 Frequency of responses (A) and scores (B) of female and male razorbill (17 pairs) to the presentation of a predator (Great black-back gull) model at two distances (1m and 3 m). Means ± SE are shown.

5.5 DISCUSSION

In their analysis of sexual size dimorphisms in shorebirds and other birds Jehl & Murray (1986) concluded that in monogamous species intersexual divergence in morphology has been accompanied by the evolution of large differences in bill length, whereas in polygamous species sexual selection has acted to maximize differences in overall size. In truly monogamous species where opportunities of re-mating (i.e. shorebirds) do not exist or is rare (i.e..alcids), the selection for larger bill dimensions may persist for different reasons (e.g. feeding roles, defense). For instance, in the North Island Kaka Nestor parrot (*meridionalis septentrionalis*), disproportionately differences in bill length of males have been attributed to male prolonged provisioning of females and young (Moorhouse *et al.* 1999). Other possible explanation is that larger bills could confer an advantage during aggressive encounters. Contestants with greater fighting ability (i.e. larger size) win fights in several species where the payoffs of winning are assumed to be high (e.g., fish: Schuett, 1997; birds: Björklund, 1989; Petrie, 1984; mammals: Clutton-Brock *et al.* 1979; Haley *et al.* 1994).

We found that bill dimensions (i.e. culmen and gape length) were significantly greater in males of both species (tables 1 & 2). Only male murres were found to be significantly heavier than females (table 1). These results concurred with previous measures of thick-billed murres (see review by Gaston & Hipfner 2000) and razorbills in different locations (Wagner 1999; Grecian et al. 2003). Larger bill dimensions in males have also been

reported in other alcids (Corkhill 1972; Nelson 1981; Jones 1993). In male crested auklets *(Aethia cristatella)*, large and hooked bills has been suggested to be sexual selected (male-male) for weaponry (Jones 1993). Larger bill dimensions may also confer males a better ability for defending or protecting the offspring. Fraser et al. (2002) suggested that male crested auklets take the brooding role because they are more aggressive and have a larger and stronger hooked bill than their mates, and therefore better equipped than females to guard young chicks or the breeding site.

According to parental investment theory, nest defence should increase during the course of a breeding season because the fitness value of a chick is higher than that of an egg and increases with time (Williams 1966; Trivers 1972; review in Montgomerie & Weatherhead 1988). Razorbills and murres are single-brooded species, so the value of the chick and the willingness to defending it should increase as breeding site departure approaches. In razorbills, as expected, I found higher levels of aggressiveness during brooding compared to during incubation. Although I was not able to collect brooding period data to make the same comparison for murres, studies at Coats Island indicated that thick-billed murres increased the amount of aggression at the time of hatching (Kober & Gaston 2003).

During the incubation period, I found sex differences in the frequency of aggressive interactions in thick-billed murres only. These results may be explained by the differential likelihood of aggressive interactions between species; murres breed in higher density colonies than razorbills. High-density nesting might impose selection for an

enhanced capacity to nest defence in one or both sexes and therefore favour larger body sizes (Jehl & Murray 1986). Only male murres were found to be significantly heavier than females (Table 5.1). Incubating murre females have more aggressive interactions than males; however males initiated most of the aggressive interactions while female aggressive behaviour was mostly responses to attacks from both conspecifics and heterospecifics (mostly neighbouring common murres). In dark-eyed juncos (*Junco hyemalis oreganus*), individuals likely to win an aggressive interaction were more likely to initiate that interaction (Jackson 1991). This also implies that chicks being protected by females (receivers) may be more often in danger than when they are with the males (initiators). Measurements of the intensity of aggressive behaviour did not indicate a sex difference in either murres or razorbills during their incubation periods.

During chick-brooding, male razorbills showed higher frequency of aggressive responses to the presence of intruders than females. However, no sex differences were found in the intensity of their aggression. This was true whether the intruder was a hetero-specific (murres, puffins) versus a conspecific. Nevertheless, male razorbills performed significantly more high-scored aggressive behaviours than females during brooding.

Predators represent a more serious threat for the egg/chick and potentially adult survival (Patterson *et al.* 1980; Stenhouse *et al.* 2005; Margalida & Bertran 2005) so responses to predators were expected to be stronger than for con-specifics or non-predator intruders. Many bird species respond differentially to different predators, likely

in accordance with the danger they pose (Patterson *et al.* 1980; Gochfeld 1984). Similar to my findings, territorial limpets, *Lottia gigantean,* show different forms of aggressive responses to con-specific intruders compared to predators (Stimson 1970). My simulated predator experiment used the most common avian predator at the Gannet Islands, great black-backed gull, presented in a natural manner, walking toward the breeding site. My results indicated a clear differential response of male and female razorbill to the presence of a predator-model. Males responded aggressively more often than females to the presence of the predator model at both distances (3m and 1m). On average, male razorbills' responses to the predator model had higher aggressive scores than those of females at both distances. These differences were mainly due to the higher frequency of negative responses (i.e. move away from or abandon chick) or lack of responses by females. In contrast to conspecific intruders, there were no high-scored aggressive responses to the predator model. In addition to the aggressive responses, razorbills also performed chick protective behaviours (i.e. moved towards chick, accommodated chick under wings); these behaviours were primarily performed by males.

In a review of nest defence behaviour, Montgomerie and Weatherhead (1988) proposed several explanations for male-biased aggressive behaviour in birds. The "perception of risk hypothesis" predicts that females in poor body condition, weakened by the rigours of nest building and egg production, will be willing to risk less in nest defence. The "renesting potential" hypothesis predicts that in male-biased populations females will have a higher chance of re-nesting if their mate is lost and therefore invest less in the current offspring defence. The "life history characteristics" hypothesis predicts

that in populations with different mortality rates, more intense nest defence can be expected from the sex that suffers a higher over winter mortality because its loss in residual reproductive value (i.e., the risk involved in nest defence) will be lower. Finally, according to the "ability to raise offspring unaided" hypothesis, if there are sex differences in the ability to raise the brood alone, then the parent taking the risks will invest less because they have more to loose for a given level of nest defence (e.g. Regelmann& Curio 1983). None of these hypotheses appears to explain the sex differences in parental aggression found in thick-billed murres and razorbills. There was no evidence for sex differences in body condition during the brooding period in thick-billed murres (Paredes *et al.* 2005). Similar survival rates have been reported for male and female thick-billed murres at Coats Island (Gaston *et al.* 1994). However, lower male survival rates for breeding common murres have been reported in Witless Bay (Robertson *et al.* 2006). Adult sex-ratio is unknown for most seabirds but generally assumed to be equal; e.g., thick-billed murres had an even sex ratio in a 2004 oil event in Newfoundland, where most likely birds of Gannets Islands spend the winter (Robertson et al. 2006.. Finally, sex-biased ability in raising the chick un-aided at an early stage is not applicable for these species because chick survival depends on both parents' care. Later on, males raise the chick on their own at sea, so their lower investment in offspring defence might be expected at the breeding site but the contrary was found. I thus proposed that male-biased breeding site defence found in murres and razorbills (Paredes *et al.* 2006) are associated with their more aggressive behaviour and greater ability (e.g. larger body size) to protect the offspring than females.

At breeding site departure, chicks typically call, walk towards the edge of the cliff/rockery, jump and attempt to fly/glide to the ocean below. They may be accompanied by the parent, a group of adults or alone. Chick mortality occurs as a result of injuries from the jump, failure of parent-offspring reunification, predation, and attacks from con-specifics (Gilchrist & Gaston 1997). The timing of chick departure, usually late evening, is believed to have evolved in response to avoidance of terrestrial and avian predators. At this time, low light conditions supposedly make it difficult for sight-hunting predators to locate departing chicks (Tuck 1960). Gull, *Larus spp.*, and fox predation seems to be the main cause of fledging failure of murre and razorbill chicks crossing beaches or rock slopes to reach the sea (Williams 1975; Hatch 1983; review by Hipfner & Chapdelaine 2002). At colonies where chicks jump directly to sea, attacks from con-specifics attracted by chick calls are a major cause of departure failure (Gilchrist & Gaston 1997). In either case, defence of the chick during departure and while at sea is crucial for its survival and therefore parents' fitness. The larger and/or better equipped and more aggressive sex would likely to be more successful protecting the chick at the colony and at sea

In several shorebirds where the male take care of the chick after female desertion, males show higher aggressive behaviour than females during the incubation and/or brooding period and few of them are also larger in body size (Table 3.). Differential aggressive behaviour between the sexes may be a key factor for understanding the division of parental roles in alcids, shorebirds and other bird species.

Table 3. Sex differences in bill dimensions and aggressive behaviour in shorebirds and alcids with biparental care and male-only care.

	Parental care duration	Culmen size	Territory/nest defence incubation	Territory/nest defence brooding	*References		
					Parental care	bill size	Parental defence
SHOREBIRDS							
American avocet (*Recurvirostra americana)*	M ≥ F	M > F	M > F [2]	-	13, 2	1	2
Black-necked Stilt (*Himantopus mexicanus)*	M ≥ F	M = F	M > F [2]	-	6, 2	1	2
Eurasian Lapwing (*Vanellus vanellus L.*)	M ≥ F F ≥ M	M = F	M > F [1]	M > F [1]	4, 6	6	5, 24
Eurasian Curlew (*Numenius arquata*)	M ≥ F	F ≥ M	-	M = F [2]	3, 21	21, 6	22
Kentish plover *(Charadrius alexandrinus)*	M > F	M = F	-	M > F [2, 3]	15	6	8*
Greater Golden plover *(Pluvialis apricaria)*	M > F	M = F	-	M > F [1]	4	6	22
Purple Sandpiper (*Calidris maritime*)	M > F	F ≥ M	M > F [1]	n/a	16,12	6, 16	12
Killdeer *(Charadrius vociferus)*	M > F	M = F	M > F [1]	M > F [1, 2]	17	6	18
Eastern willet (*Catoptrophorus Semipalmatus*)	M > F	M = F	-	M > F [1]	19	6	19
Malasyan plover (*Charadrius peronii*)	M = F	-	M > F [1]	M = F [1]	20	-	20
Black-tailed godwit (*Limosa limosa L.*).	M = F	M = F	M > F	M > F	14, 6	6	5
ALCIDS							
Thick-billed murre *(Uria lomvia*)	M > F	M > F	M > F [1]	-	7	This study	This study
Razorbill (*Alca torda*)	M > F	M > F	M = F [1]	M > F [1, 2]	7	This study	This study

Parental care duration: M ≥ F: biparental or biparental plus male-only care, M = F: biparental care, F ≥ M: biparental care or biparental plus female-only care.
[1] Observations, [2] Predator-model experiment, [3] Mate removal experiment (measure of chick survival).
* High density colony (no sex differences in chick survival in low density areas; Székely *et al.* 2006).
n/a : not applicable because females desert the nest right after hatching.

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*References 1, Hamilton (1975); 2, Sordahl (1990); 3, Reynolds & Székely (1997); 4, Nethersole-Thompson (1986); 5, Hehgy & Sasvari (1998); 6, Johnsgard (1981); 7, Gaston & Jones (1998); 8, Székely (1996); 9, Creelman & Storey (1991); 10, Brunton (1988); 11, Fraser *et al.* (2002); 12, Pierce (1997); 13, Gibson (1971); 14, Lind (1961); 15, Székely & Lessens (1993); 16, Cramp (1983); 17, Lenington (1984); 18, Brunton (1990); 19, Howe (1982); 20, Yasué & Dearden (2007), 21, Curie *et al.* (2001); 22, Byrkjedal (1987); 23, Jones (1993).

In summary, males were larger in body mass (only murres) and bill measurements than females. Frequency but not intensity of aggressive behaviour against con-specifics was higher in males of both species (murres: incubation; razorbills: brooding). Both frequency and intensity of aggressive responses to a predator model was higher in male razorbills. Altogether, my results suggest a male-biased capacity for protection of the chick in murres and razorbills. These findings may partially explain why the male is the selected sex to accompany the chick at sea.

5.6 ACKNOWLEDGMENTS

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CHAPTER 6: PARENTAL ROLES OF MALE AND FEMALE THICK-BILLED MURRES AND RAZORBILLS AT THE GANNET ISLANDS, LABRADOR

6.1 ABSTRACT

I studied female and male parental roles in two sympatric auks, thick-billed murre, *Uria lomvia*, and razorbill, *Alca torda*, with initial biparental care at the breeding site and later exclusively paternal care at sea. My study addressed the following two questions: Why do males accompany chicks to sea?, and How do the sexes allocate parental effort at the breeding site before parental care at sea begins? I tested the hypothesis that males care for chicks at sea because they are in better condition at the time of chick departure as a result of female-biased parental effort at the breeding site ('nest'). Breeding success and duration of chick-rearing did not differ between the two study years in either species at the Gannet Islands, Labrador. At the breeding colonies, females of both species provided more food (murres: 2.84 ± 0.18 loads day $^{-1}$; razorbills: 2.02 ± 0.11 loads day $^{-1}$) to their chicks than males (murres: 2.26 ± 0.12 loads day $^{-1}$; razorbills: 1.42 ± 0.09 loads day $^{-1}$), and males spent more time brooding the chicks. These differences were chick-age dependent in both species, with females providing more meals to chicks older than two

weeks. Razorbill males spent more time with chicks greater than two weeks old, while murre male's attentiveness of brooding did not vary with chick age. In both species, males (murres: 3.04 ± 0.3 h day^{-1}; razorbill: 3.30 ± 0.2 h day^{-1}) performed longer foraging trips with meal delivery than females (murres: 1.23 ± 0.4 h day^{-1}; razorbill: 2.50 ± 0.4 h day^{-1}). Thick-billed murres showed a consistent diurnal pattern of egg and chick attendance: females were usually found at the breeding site during the day whereas males were found there early in the morning and at night. In contrast, razorbill's timing of attendance was much more variable and did not differ between sexes. Despite these differences in timing of breeding site attendance between species, males of both species spent twice as much time as females engaged in the defence of the egg or chick at the breeding site, which suggest male-biased capability of protecting the chick at departure. Overall my data indicated different female and male parental roles at the breeding site but not a female-biased allocation of time, energy and risk as predicted. In fact, males seem to provide equal if not more parental effort than females prior to the time of colony departure. I propose that the patterns of parental roles found between sexes is the result of a chain of events favouring male involvement in chick brooding and care at sea.

6.2 INTRODUCTION

Decision-making about allocation of energy, time and risk is an ongoing task for animals during reproduction and it is believed that natural selection acts against individuals that fail to balance tradeoffs associated with these decisions. The allocation of resources between current and future reproduction is the crucial life-history trade-off (Williams 1966), and long-lived species should maximize lifetime fitness by balancing current and future costs and benefits of reproduction (Stearns 1992). In nature, excessive reproductive effort at one breeding attempt may greatly decrease individuals' lifetime reproductive success in long-lived seabirds (Croxall & Rothery 1991; Wooller *et al.*1992). In monogamous species such as seabirds, biparental care is obligatory because a lapse of one parent's contribution leads to breeding failure. Although biparental care is necessary for success in such species, the level of contribution toward specific duties, or parental roles, may vary between sexes. (Trivers 1972; Bart & Tornes 1989).

The members of the avian family Alcidae are a diverse group of diving birds with remarkably variable forms of parental care and stages of chick development at the time of chick departure from the breeding site. At one end of the spectrum, puffins (*Fratercula* sp.), guillemots (*Cepphus* sp.) and *Brachyramphus* murrelets provide biparental care at the nest site until chicks are nearly fully grown ("semi-precocial"; Sealy 1973) and fledge

unaccompanied by their parents. At the other extreme, *Synthliboramphus* murrelets depart with their chicks two days after hatching ("precocial"; Sealy 1973), and both parents provide care at sea. In the tribe Alcini, thick-billed murres, *Uria lomvia*, common murres, and razorbills, *Alca torda*, have a short period of biparental care at the breeding site (15-20 days) and partly grown chicks (15-30 % of adult body mass; "intermediate"; Sealy 1973) depart with the male parent to sea for an additional 3-4 weeks of exclusively paternal care (Gaston & Jones 1998). Partly grown dovekie chicks, *Alle alle,* the fourth Alcini member, also depart the colony with their male parent (27 days after hatching; Stempniewicz 1995; Harding *et al.* 2004), but with 68-72% of adult body mass ("semiprecocial", Sealy 1973; Norderhaug 1980; Stempniewicz 2001; Harding *et al.* 2004).

The most common explanation for the evolution of departure to sea of the partly-grown chicks of the Alcini tribe is the constraint on provisioning at the colony imposed by the load-carrying capacity (Houston *et al.* 1996; Gaston & Jones 1998). These large auks have the highest wing loading of all seabirds (Greenwalt, 1962; Spear & Ainley, 1997), which is a tradeoff for having excellent diving capacity. Consequently the flight costs of foraging and meal delivery are energetically expensive. However, this limitation should not apply so much to the much smaller planktivorous dovekies, and its applicability to razorbills that provision their chicks with multiple (sometime large) fish is questionable. Another explanation for early chick departure is that predation risk is high at the colony compared to at sea (Cody 1971; Ydenberg 1989; Ydenberg *et al.* 1995). Ydenberg's (1989) model for the intermediate-fledgling alcids assumed that chicks have a lower

mortality rate at the colony than at sea, but grow faster at sea than at the colony. Neither of these two assumptions are rigorously testable (i.e. logistical limitations) and more importantly, this 'tradeoff' hypothesis has no exclusive predictions (Gaston & Jones 1998).

It is also important to keep in mind that males play the dominant role in raising chicks in many other species of Charadriiformes. For example, in socially monogamous scolopacids, females attend chicks for a shorter period after hatching than do males, and may even desert late in incubation (Gratto-Trevor 1991; Piersma 1996a; Payne & Pierce 2002). A similar but weaker trend also occurs in socially monogamous Charadriids (Piersma 1996b). Therefore, a functional explanation for paternal care late in chick development specific to auks of the tribe Alcini may not be required. In this paper I take as a starting point only that 'intermediate' chick colony departure is a phylogenetically fixed characteristic of the auk tribe Alcini.

Despite the different stages of development at chick departure, modes of chick provisioning, and nest-site characteristics (murres: open nests; razorbills: open and crevice nests; dovekies: crevice nests), the four Alcini members share a unique "intermediate" form of parental care; biparental care at the breeding site and uni-male parental care at sea. Two interesting questions that arise from patterns of parental care among the auk species are: Why do males accompany chicks to sea?, and How do the sexes allocate parental effort at the breeding site before paternal care begins when the chick departs the colony? By understanding how sexes distribute energy allocation at the breeding site may help to explain their partitioning of roles after chick-departure.

Differences in energy expenditure due to different female-male constraints at the breeding site may cause one sex to be in better condition and thus better able to finish raising the chick at sea. For instance, different mortality rates (Nelson 1978), population ratios (Tershy & Croll 2000), foraging strategies (Markman *et al.* 2004), and aggressive behaviour (Burger 1981; Fraser *et al.* 2002) are some factors that appear to affect the division of parental roles and effort allocation between sexes in biparental care species. It has been suggested that the risk of loss of paternity can limit the allocation of male parental effort; so males should invest parentally in proportion to their probability of siring their mates' young (Trivers 1972; Maynard Smith 1977). Although both sexes guard their mates in an effort to assure paternity and to maintain pair bonds, extra-pair copulations and, to a lesser degree successful fertilizations occur in murres (thick-billed murres: Gaston & Hipfner 2000; common murres: review by Ainley *et al.* 2002) and razorbills (Wagner 1992). Before egg-laying (3-4 weeks), males are continuously present at the breeding site (common murres) and/or mating arenas (razorbills) while female visitation is occasional (Gaston & Jones 1998). By doing this, males seem to reduce their uncertainty of paternity and potentially increase the number of offspring they father (Gaston & Jones 1998). However, during this time males engage in fights and are likely to fast or have reduced opportunities to feed (Birkhead *et al.* 1985), so overall they should have higher risk and energy costs than females. Theoretical models predict conflicts of interest in the level of parental effort between sexes, so in some circumstances each parent's fitness can be enhanced at the expense of their partner's

effort (Houston & Davies 1985; McNamara *et al.* 1999). On the other hand, individuals in species with long-term monogamy, such as the murres (review by Gaston & Hipfner 2000; review by Ainley *et al.* 2002) and razorbills (review by Hipfner & Chapdelaine 2002), are expected to be less likely to exploit their partners because maintaining their partners' condition enhances the fitness of both parents (review by Mock & Fujioka 1990; Fowler 1995). Thus, individuals of species with long-term pair bonds may distribute parental effort such that the partner who will benefit the most from contributing less parental effort does less work (K. M. Jones *et al.* 2002). I hypothesize that a male's effort at the breeding site will be lower than a female's because of the male's initial energy expenditure guarding their mate prior to egg laying. On the other hand, female auks produce a relatively large egg, from which hatches a semi-precocial chick (Cramp 1985). This initial parental investment, although costly, may influence the female's decision to compensate for their partner's reduced parental effort at the breeding site. As a result, males might be in better condition than females to finish raising the chick at sea.

Both murres and razorbills are central place foragers so they have to commute several times a day between their nests and foraging areas to feed their chicks. Foraging is energetically expensive for these flapping-flight and pursuit-diving species (Birt-Friesen *et al.* 1989; Obst & Nagy 1992; Bech *et al.* 2002; Jodice *et al.* 2003). Thus, foraging for chick provisioning must be more costly than incubation/brooding at the colony. Taking all these factors into consideration I predict that early in the chick-rearing period, males might allocate most of their time at the breeding site, and females would spend most of their time foraging for chick provisioning. Equal parental investment in

breeding site defence before chick departure is expected for both species. After chick departure, males will provide all the care for several weeks but will not have the additional effort of flying for chick feeding as they raise the chick at their feeding grounds (Gaston & Jones 1998).

The aim of this study is to compare two sympatric Alcini species with similar chick-rearing behaviour, to determine intra and inter-specific patterns in parental behaviour between sexes. Thus, I examined four components of parental care: breeding site attendance (egg/chick care and breeding site defence), provisioning rates, prey size delivered to chicks, and foraging trips. This allowed me to quantify the contribution of both sexes to parental care at the breeding site of thick-billed murres and razorbills at the Gannet Islands, Labrador.

Understanding how males and females distribute parental roles may give us insights into how evolution has shaped forms of parental care, the extent to which morphological, physiological and behavioural factors limit the allocation of parental effort, and why the transition to paternal care at sea occurs in the first place.

6.3 METHODS

Behavioural observations were undertaken during the incubation and chick-rearing periods (June-August) of thick-billed murres (2000-2001) and razorbills (2001-2002) at

GC4, one of the six Gannet Islands located on the low arctic coast of Labrador, Canada (53°56'N, 56°32'W).

I studied a total of 15 thick-billed murre pairs and 31 razorbill pairs. Both groups were located in the same cliff area ("Grey Cup") on the north side of the island with about 150 and 45 open breeding sites of murres and razorbills respectively. Behavioural observations were undertaken from a blind, using a zoom telescope (20-60x, 60 mm) and binoculars (10x, 50 mm), between dawn to dusk (0400h - 2200h; sunrise occurred between 0330h and 0400h and sunset between 2130h and 2200h). Two observers made daily observations in double shifts of 4.5 h each with an equivalent resting time in between shifts. Most birds were already incubating eggs when I started the observations the period of observation covered most of incubation (9-27 days post-laying) for razorbills and half of incubation for thick-billed murres (7-15 days post-laying) except when egg loss occurred. Observations continued through hatching until chicks were fledged. Hence, observations covered most of the brooding period in both species (6-16 days for razorbills, and 5-15 days for murres), except in cases of breeding failure.

Individuals were identified by temporary marks of picric acid (yellow) or fluorescent paint (green, pink and orange) delivered from a small container (10 ml of the marking liquid) attached to the tip of a 4 m graphite pole. This method allowed marking from above the birds without disturbing the colony. The birds' reaction to the marking liquid was similar to that produced by falling guano, which is a normal occurrence in the colony, so additional disturbance caused by marking was minimal. Identifying marks and life history information of individuals were recorded on cards for quick reference.

Breeding sites were scanned every 10 minutes and the presence or absence of marked birds was recorded so that the time spent at the breeding site per day could be calculated. When both adults were present, the "off-duty" parent was observed interacting aggressively with conspecifics and predators (great black-backed gulls, *Larus marinus*), and also preening their mates (Paredes *et al.,* unpublished data), so I assumed birds were mainly engaged in the defence of the breeding site, mate and offspring. The identity of the adult incubating or brooding ("egg/ chick care") and that of the "off-duty" parent ("breeding site/mate defence") was recorded and the time spent in these activities calculated separately. The departure and arrival times of adults, and chick provisioning events, were recorded continuously to quantify chick provisioning frequencies and foraging trip durations. During chick provisioning, I identified prey items to the species level when possible, recorded the number of items per load, and estimated the length of prey items when possible. I used direct estimation of the prey items' length compared to the length of the gape as a reference unit for estimating prey size (e.g. two-times gape length). Then, I used the mean gape length of males and females to estimate the prey item length in centimeters. A similar method of prey length estimation was used by Gaston & Nettleship (1981) but using the culmen as a reference unit.

One member of each pair was captured during the chick-rearing period for permanent marking and sex determination. Murres were captured with a noose of nylon monofilament (1.5 mm diameter) on the end of a 4-m graphite pole. Razorbills were captured with a small weighted noose-carpet attached to one end of 20 m of nylon monofilament line (1.5 mm diameter) and with the other end attached to 3-m wooden

pole. The noose end was positioned on cliff ledges used by the birds, so they were captured by the leg as they approached or departed their breeding site. Birds were marked with a field readable stainless steel leg band and a colour band. Blood samples (0.5 ml) were taken from the tarsal vein and stored in 95% ethanol for sex determination using molecular DNA analysis (Fridolfsson & Ellegren 1999). The results of sexing were obtained after the season was finished (observers were blind to the sex of birds) and then matched with the ID cards to interpret behavioural data.

Every year, I followed a large number of thick-billed murres, (49-50 pairs) and razorbills (36-41 pairs), including the birds used for behavioural observations and for breeding success determination. Pairs were followed from incubation to chick departure to determine overall breeding success (proportion of eggs that survived to chick departure per active breeding site), fledgling success (proportion of chicks that fledged per active breeding site), and the duration (days) of the brooding period.

6.3.1 Data analysis

Two years of behavioural data (breeding site attendance: egg/chick care and breeding site/mate defence, chick provisioning, and foraging trips) and chick diet (species and size) were pooled for each species for the analysis of parental care because no differences in breeding success and duration of chick-rearing were found between years (see below). For each individual, I quantified time spent at the breeding site per 24 h. Even though the

observation period only covered daylight hours (c. 18 h), previous studies have shown that male and female thick-billed murres at the Gannet Islands do not make parental roll changes ("change-overs") at night (Jones *et al.* 2002). In this study, most of the same birds present at dusk were present the following morning with soiled plumage, suggesting they did not leave the breeding site during the night. In addition, I did not see flight activity of murres or razorbills at the colony during opportunistic observations in moonlight conditions during the night. Consequently, I added six hours (dark time) to individuals present at dusk and dawn at the breeding site. The initial sample size of murre ($N = 15$) and razorbill ($N = 31$) pairs used for the behavioural analysis of the incubation period decreased slightly during the brooding period because of breeding failure. I did not include data from new pairs, except for the analysis of prey species delivered to chicks between sexes to be able to find possible differences in second prey items. Only 1/15 murre pairs and 5/31 razorbill pairs were followed during the two study years. Because of the small ratio of repeated pairs, I believe that possible data duplication, assuming birds behaved the same in both years, might have not affected the statistical analysis. However, I tested for possible effect of data duplication in razorbills by excluding one-year of data (randomly chosen) of replicated pairs and compared these results with those of complete data. Female razorbills spent longer time incubating (12.90 ± 0.30 h day $^{-1}$) than males (11.10 ± 0.30 h day $^{-1}$) when one-year data of repeated pairs was excluded (Paired t-test: $t_{1, 25} = 3.049$, $P = 0.005$) and when it was not (see below). I did not use data from repeated individuals for independent statistical tests.

I calculated the number (shifts day $^{-1}$) and duration (h shift $^{-1}$) of incubation and brooding shifts for each species using the total number of days of observation per period. The time spent at the breeding site ("breeding site attendance") was sub-divided into time spent incubating or brooding the chick ("chick care"), and off-duty time. Breeding site and sub-categories of attendance were analysed separately for each sex and pair-wise per breeding site. The timing of breeding-site attendance by males and females was calculated using hourly checks for attendance of the egg or chick (24 h period) during the incubation and brooding period. Timing of chick provisioning was calculated based on the total number of feedings of males and females recorded during the brooding period.

Chick provisioning rates (loads individual $^{-1}$ day $^{-1}$), total number of trips (number individual $^{-1}$ day $^{-1}$), and duration of foraging trips (h individual $^{-1}$ day) were averaged per individual across three chick-age groups (one, two, and three weeks old). These data were analysed using two-way ANOVAs with sex and chick-age group as the main factors. In addition, paired comparisons were undertaken between sexes matched per breeding site to control for individual differences and confirm results from the cross-sectional analysis. Load sizes were also determined and compared between sexes in both species (as was number of prey items per load for razorbills). It was not possible to distinguish between bathing trips and feeding trips because birds could return to the breeding site with a fish after absences of less than 10 minutes. All foraging trips ("total") and those with meal delivery ("w/meal") were analysed separately so results could be related to parental care. The first foraging trip was usually performed by females, which normally spent the night at sea (Jones *et al.* 2002) and arrived at the breeding site in the early morning. Thus, in

order to calculate the duration of the first foraging trip I assumed birds started to forage right after sunrise (0330h). This assumption is supported by large number of murres and puffins observed on the water just before dawn at Witless Bay, Newfoundland (Schneider *et al.*1990).

6.3.2 Statistical analysis

Statistical analysis was carried out using SPSS version 11.5. I used parametric tests (ANOVA, Student *t*-test for independent samples, and paired *t*-test) to compare groups if the residuals met the assumptions for the general linear model. If not, I transformed data and checked whether the residuals met the assumptions for the transformed response variable. For instance, data of foraging trip duration was log-transformed before statistical analysis to reduce skewness and variance of the means. Chi-Square tests with Yates's correction were used to compare proportions. Means were expressed ± SE of the mean. All comparisons were two-tailed, and differences were considered significant when $P < 0.05$.

6.4 RESULTS

6.4.1 Breeding success and duration of chick-rearing period

The reproductive success of murres (2000: 0.55 fledglings breeding site $^{-1}$, $N = 49$; 2001: 0.74 fledglings breeding site $^{-1}$, $N = 50$); and razorbills (2001: 0.85 fledglings breeding site $^{-1}$, $N = 41$; 2002: 0.72 fledglings breeding site $^{-1}$, $N = 36$) did not differ significantly between years (murres: Student t-test: $t_{97} = -1.99$, $p = 0.05$; razorbills: Student t-test: $t_{75} = 1.41$, $p = 0.16$). Of the murre's eggs that hatched, a similar proportion survived to chick departure in both years (2000: 0.93 fledglings breeding site $^{-1}$, $N = 29$; 2001: 0.97 fledglings breeding site $^{-1}$, $N = 38$; Student t-test: $t_{65} = -0.83$, $p = 0.41$). Similarly razorbill's fledging success did not differ between years (2001: 0.97 fledglings breeding site $^{-1}$, $N = 36$; 2002: 1.00 fledglings breeding site $^{-1}$, $N = 26$; Student t-test: $t_{60} = -0.85$, $p = 0.40$). In 2000, murres lost more eggs than in 2001 for unknown reasons, which may explain the marginal p value (0.05) for the overall breeding success in 2000.

The duration of the chick-rearing period for murres (2000: 19.88 ± 0.48 days, $N = 17$; 2001: 20.33 ± 0.80 days, $N = 18$) and razorbills (2001: 18 ± 0.8 days, $N = 19$; 2002: 19 ± 0.60 days, $N = 10$) did not differ significantly between years (murres: Student t-test: $t_{33} = -0.48$, $p = 0.63$; razorbills: Student t-test: $t_{27} = 0.84$, $p = 0.41$). For these reasons, data from the two study years were pooled for the analysis of parental care in each species.

For both murres ($N = 13$) and razorbills ($N = 21$), all birds that were seen departing with a chick were males as confirmed by DNA analysis (Fridolfsson & Ellegren 1999).

6.4.2 Breeding site attendance

6.4.2.1 *Thick-billed murres*

The mean number of change-overs per day during incubation was 3.24 ± 0.07 (range 2 – 7) with three change-overs on most days (63%, $N = 164$). Occasionally two (14%) change-overs occurred per day, otherwise there were four (12%) or more (11%). The duration of incubation bouts varied from 0.67 to 22.33 h. On average, the duration of the first, second and third incubation bouts were 2.73 ± 0.17 h, 10.98 ± 0.36 h and 8.25 ± 0.30 h, respectively. The first and third bouts were usually performed by males and the second by females.

Most males incubated eggs early in the morning (0400h – 0600h) and late afternoon and night (1900h - 0300h); while females incubated eggs mostly during the day and early afternoon (0800h - 1700h; Figure 6.1). On average, males spent significantly more nights incubating eggs (8.9 ± 1 days, $N = 15$; paired t-test: t 12 = -6.775, $P < 0.001$) than females (1.3 ± 0.36 days, $N = 15$). During the incubation period, male murres (14.66 ± 0.51 h day -1, $N = 15$) spent significantly more time at the breeding site than their female mates (12.14 ± 0.32 h day -1, $N = 15$; paired *t*-test: $t\ 14 = -3.15$, $P < 0.01$). Even

though the sexes did not differ in the daily amount of time allocated to incubate their eggs (paired *t*-test: t 14 = -1.75, $P = 0.10$), males devoted more time to certain other activities (e.g., breeding site defence and mate preening) at the breeding site than females (paired *t*-test = t 14 = -4.75, $P < 0.001$; Figure 6.2).

The mean number of change-overs per day during the brooding period was 5.34 ± 0.2 (range 3 - 12), with 40% of 101 days having five change-overs, 21% three, 13% seven, 9% four, and 7% six. The overall mean duration of brooding bouts was 4.49 ± 0.18 h (range 0.17 - 17.17 h). The mean duration of the first, second, third, fourth and fifth chick-rearing bouts were 1.62 ± 0.08 h, 5.73 ± 0.36 h, 4.41 ± 0.46 h, 4.12 ± 0.41 h, 7.23 ± 0.59 h, respectively. The first and the last bout were usually performed by males. The timing of breeding site attendance of males and females during the brooding period was similar to that observed during the incubation period, except that females had earlier and shorter bouts (0700h – 1400h; Figure 6.1). Males spent significantly more nights with the chick (7.0 ± 0.49 days, $N = 13$) than females (0.92 ± 0.29 days, $N = 13$; paired *t*-test: $t_{12} = -9.013$, $P < 0.001$; Figure 6.1).

During the brooding period, male murres (15.52 ± 0.30 h day $^{-1}$, N =13) spent significantly more time attending the breeding site than their female mates (10.44 ± 0.30 h day $^{-1}$, N =13; paired *t*-test: $t_{13} = -9.1$, $P < 0.001$). Males spent significantly more time brooding their chicks than females did (paired *t*-test: $t_{13} = -8.7$, $P < 0.001$); and the additional time that each parent spent at the breeding site (i.e., when their mates were present brooding) did not differ significantly between sexes (paired *t*-test: $t_{13} = -1.93$, P =

0.08; Figure 6.2). The time spent brooding did not depend on chick age (females: ANOVA: $F_{2, 42} = 0.23$, $P = 0.79$; males: ANOVA: $F_{2, 42} = 0.13$, $P = 0.88$; Figure 6.3).

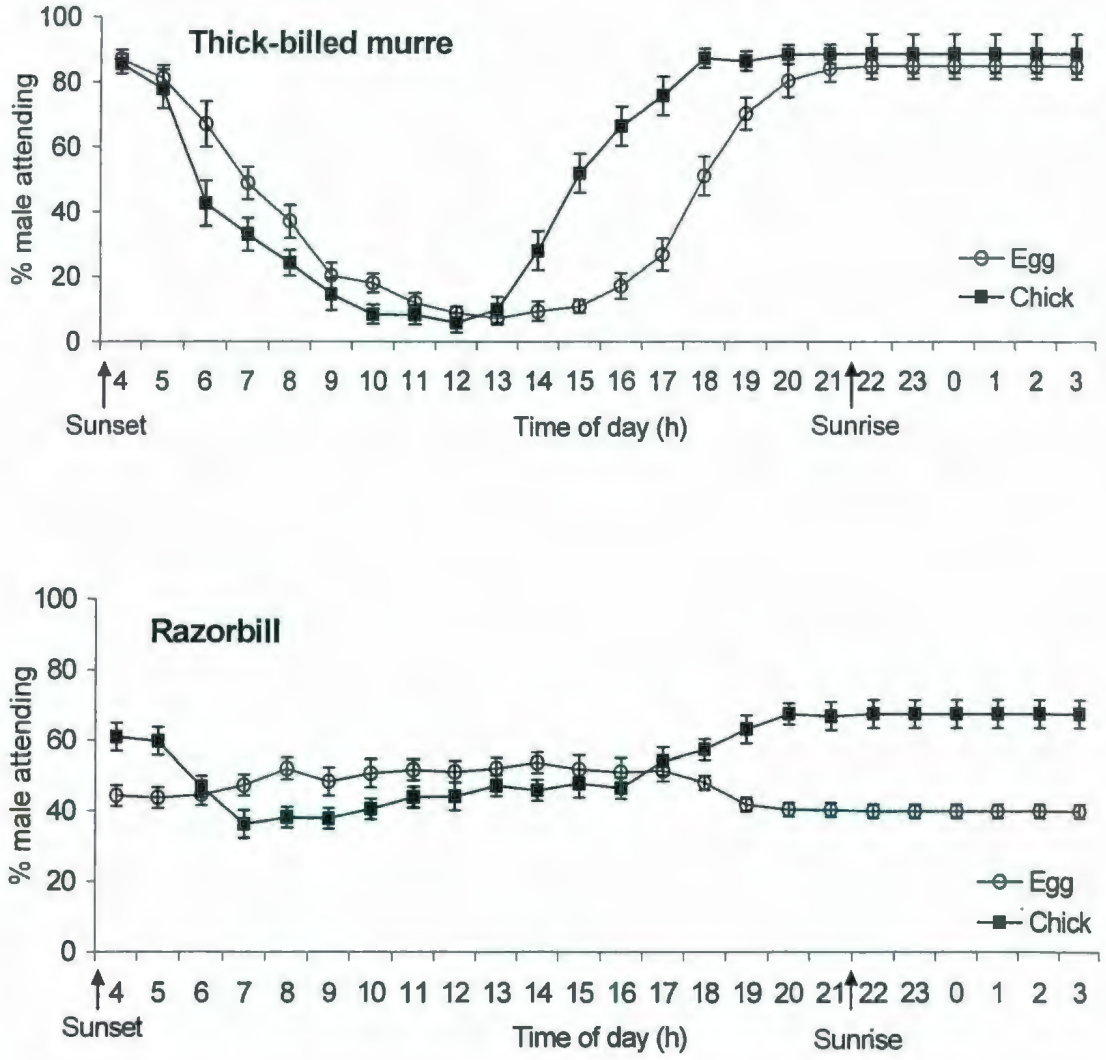

Figure 6.1 Timing of breeding site attendance of thick-billed murres and razorbills during the incubation ($N = 15$ pairs; $N = 31$ pairs) and brooding ($N = 13$ pairs; N = 23 pairs) period at Gannet Islands, Labrador. Means of males ± SE are shown.

6.4.2.2 *Razorbills*

The mean number of incubation change-overs per day was 2.90 ± 0.06 (range 1- 9). Most days razorbills had two (48%, $N = 372$) or three change-overs (30%), but occasionally had four (9%), five (7%) or more (4%). The overall mean duration of incubation bouts was 8.23 ± 0.18 h (range 0.17 - 24 h). The mean duration of the first, second, third, fourth and fifth incubation bouts was 5.43 ± 0.21 h, 12.20 ± 0.32 h, 7.39 ± 0.39 h, 6.45 ± 0.62 h, and 6.69 ± 0.68 h, respectively. Male and female razorbills were equally likely to be found at the breeding site during the day (0400h – 1800h; Figure 6.1). However, on average females spent significantly more nights incubating the egg (11.6 ± 1.17 days) than males (7.6 ± 0.74 days; paired *t*-test: $t_{19} = 3.21$, $P = 0.005$).

Overall, female razorbills (13.69 ± 0.29 h day $^{-1}$, $N = 31$) spent significantly more time at the breeding site than males during incubation (12.23 ± 0.22 h day $^{-1}$; paired *t*-test: $t_{30} = 3.02$, $P < 0.01$). These differences were mainly due to the greater amount of time females spent incubating the eggs than their mates (paired *t*-test: $t_{30} = 3.75$, $p < 0.01$; Figure 6.2). Males spent significantly more time than females in other activities at the breeding site, such as breeding site defence, (paired *t*-test: $t_{30} = -3.64$, $P < 0.01$; Figure 6.2).

During the brooding period razorbills had on average 6.06 ± 0.15 (range: 2-15) change-overs in 24 hours, with most days (64%, $N = 219$) having four to seven change-overs. The overall mean duration of brooding bouts was 3.95 ± 0.11 h (range 0.17 - 19 h). On average the first, second, third, fourth, fifth, sixth and seventh brooding bouts lasted

2.56 ± 0.10 h, 4.90 ± 0.21 h, 3.28 ± 0.22 h, 4.00 ± 0.29 h, 4.00 ± 0.36 h, 3.45 ± 0.36 h and 4.40 ± 0.49 h, respectively.

Females were at the breeding site more often between 0700h and 1000h and males between 1700h and 0500 h (Figure 6.1). In contrast to the incubation period, males spent significantly more nights with the chick (6.65 ± 0.5 days) than females (3.75 ± 0.61 days, paired *t*-test: $t_{19} = -3.28$, $p = 0.004$). Overall, razorbill males (13.41 ± 0.42 h day $^{-1}$, $N = 23$) and females (12.28 ± 0.42 h day $^{-1}$, $N = 23$) did not differ in the time spent at the breeding site (paired *t*-test: $t_{21} = -1.44$, $P = 0.17$) during chick rearing. However, time spent brooding differed according to chick age for males (ANOVA: $F_{2, 57} = 7.67$, $P = 0.001$) and females (ANOVA: $F_{2, 57} = 7.66$, $P = 0.001$; Figure 6.3). Females brooded one to two weeks old chicks significantly more than three-week old chicks (Turkey HSD: $P < 0.01$), whereas males spent significantly more time brooding three-week old chicks (Turkey HSD: $P < 0.01$). Overall, males spent significantly more time at the breeding site engaged in other activities (e.g., breeding site or mate defence) when their partners were brooding than females did (paired *t*-test: $t_{21} = -2.91$, $P < 0.01$; Figure 6.2).

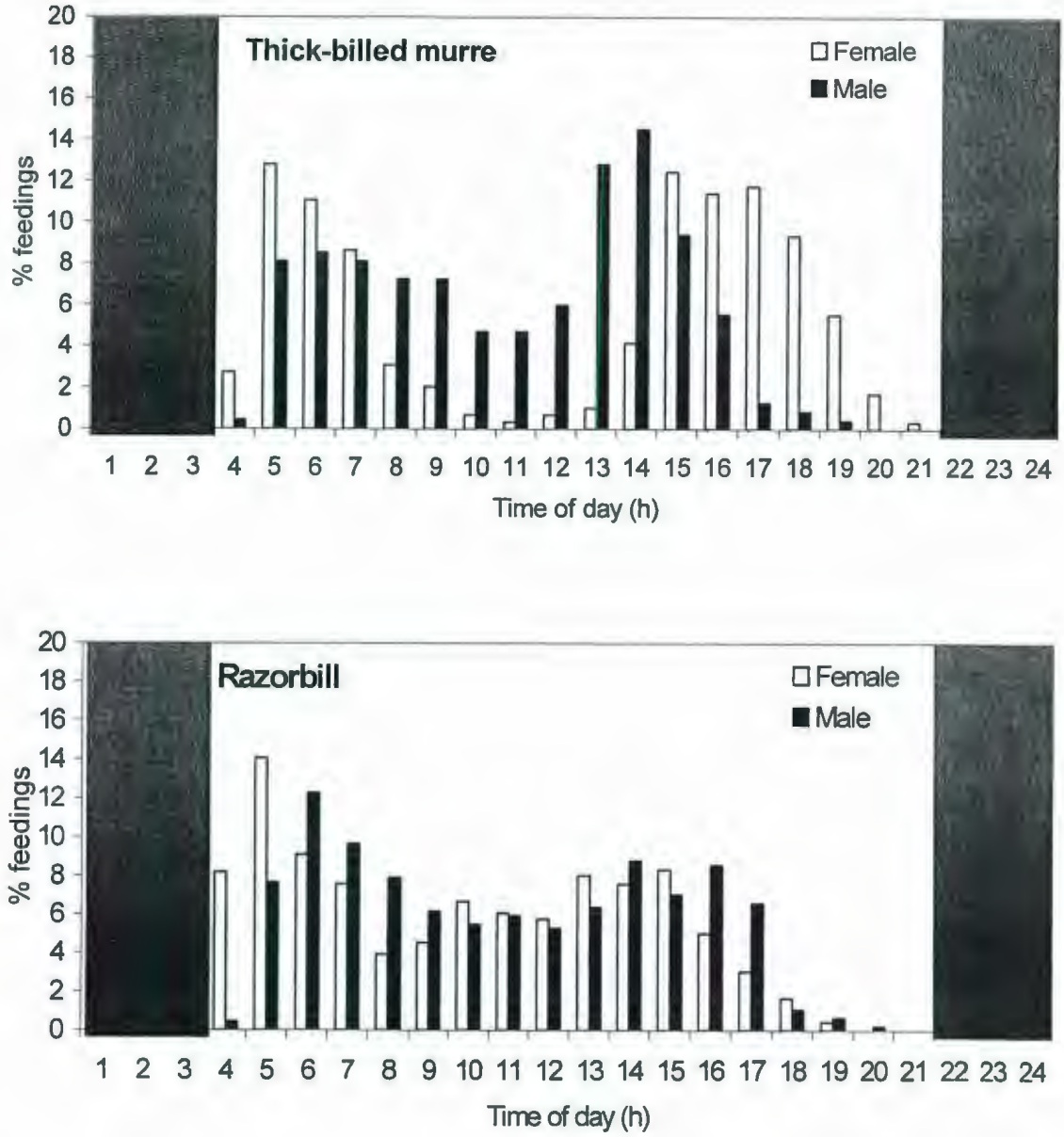

Figure 6.2 Timing of chick provisioning of thick-billed murres and razorbills at Gannet Islands, Labrador. Proportions of the total number of feedings of males (murres: $N = 235$; razorbills: $N = 456$) and females (murres: $N = 290$; razorbills: $N = 660$) are shown.

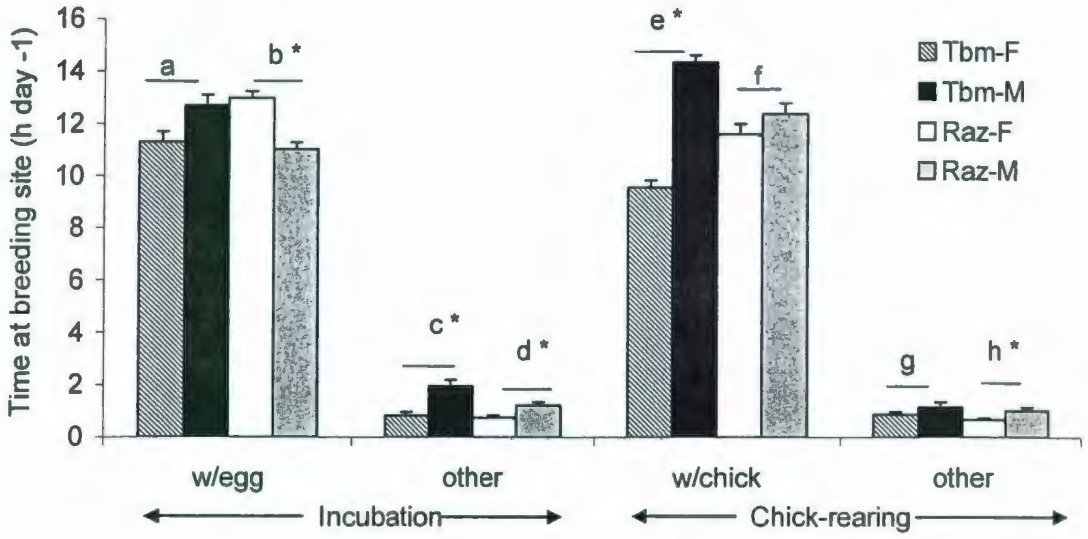

Figure 6.3 Time spent at the breeding site (Means ± SE) by male (M) and female (F) razorbills (razo) and thick-billed murres (Tbm) at Gannet Islands, Labrador. The overall time spent at the breeding site has been broken in subcategories: incubating (w/egg), brooding (w/chick) and chick/mate defence and preening (other). Only the pair comparisons between sexes "b", "c", "d", "e", and "h" were significant (* Paired *t* test: $P < 0.05$).

6.4.3 Chick-provisioning

6.4.3.1 *Thick-billed murres*

Females had a bimodal timing of chick feeding; 41% ($N = 290$ feedings) of the total feedings occurred early in the morning (04:00-09:00 h), and 51% late in the afternoon (14:00-19:00 h; Figure 6.4). In contrast, males had a single and long period of chick

feeding; 97% (N = 235 feedings) of the total feedings occurred between 05:00–19:00 h. However, 42 % of the feedings occurred after midday between 13:00-16:00 (Figure 6.4). Chick provisioning frequency differed significantly between sexes (females: 2.84 ± 0.18 loads day $^{-1}$, N = 13; males: 2.26 ± 0.12 loads day $^{-1}$, N = 13; two-way ANOVA: $F_{1, 72}$ = 7.78, P< 0.01); but provisioning frequency did not vary with chick age (one week, 2.25 ± 0.19 loads day $^{-1}$; two week, 2.76 ± 0.18 loads day $^{-1}$; three week, 2.63 ± 0.21 loads day $^{-1}$; $F_{2, 72}$ = 2.20, P = 0.12). The interaction term sex*chick age was not significant ($F_{2, 72}$ = 2.48, P = 0.06). Further analysis of the main factors showed that only the provisioning rates of females differed significantly among chick-age groups (females: ANOVA: $F_{2, 39}$ = 4.09, P = 0.03; males: ANOVA: $F_{2, 39}$ = 0.08, P= 0.93). Female murres fed their chicks significantly more often than males during the second (ANOVA: $F_{1, 24}$ = 11.01, P < 0.01) and third weeks after hatching (ANOVA: $F_{1, 24}$ = 4.94, P = 0.04), but did not differ in feeding rates when chicks were less than one week old (ANOVA: $F_{1, 24}$ = 0.12, P= 0.73; Figure 6.5). The total chick provisioning per pair did not vary among chick-age groups (ANOVA: $F_{2, 36}$ = 0.28, P = 0.09; Figure 6.5). Thick-billed murres always delivered a single prey item per load. The length of prey items was calculated based on the estimation of the gape, which was significantly larger for males (6.11 ± 0.05 cm, N = 38) than for females (5.90 ± 0.04 cm, N = 43; Student t-test: t_{79} = -3. 29, P < 0.01). The length of prey items delivered did not vary between males and females (female: 12.8 ± 0.33 cm, N = 13, male: 13.4 ± 0.16 cm, N = 13; two-way ANOVA: $F_{1, 72}$ = 2.74, P = 0.10) or chick-age group (one week: 12.8 ± 0.28 cm, N = 26; two week: 13.4 ± 0.40 cm,

$N = 26$; 13.1 ± 0.26 cm, $N = 26$; $F_{2, 72} = 0.94$, $P = 0.40$). There was no interactive effect of the main factors on the length of the prey delivered ($F_{2, 72} = 0.36$, $P = 0.70$).

6.4.3.2 *Razorbills*

Females and males fed their chicks throughout the day (04:00 – 20:00 h, Figure 6.4). Both sexes had two small peaks of prey delivery early in the morning (females: 04:00-07:00 h = 39%, $N = 660$ feedings; males: 05:00–08:00 h = 38%, $N = 456$ feedings), and early in the afternoon (females: 14:00-16:00 h = 24%; males: 15:00–17:00 h = 24%; Figure 6.4).

Razorbills delivered an average of 2.13 ± 0.08 items (range 1 – 8) per load. On average the number of prey items per load did not differ significantly between females (2.20 ± 0.11 preys load $^{-1}$, $N = 14$) and males (2.06 ± 0.11 preys load $^{-1}$, $N = 14$; two-way ANOVA: $F_{1, 78} = 0.75$, $P = 0.34$); or with chick age (one week: 2.01 ± 0.11 preys load $^{-1}$, $N = 28$; two week: 2.25 ± 0.13 preys load $^{-1}$, $N = 28$; three week: 2.12 ± 0.15 preys load $^{-1}$, $N = 28$; $F_{2, 78} = 0.79$, $P = 0.46$). There was no interactive effect of the main factors on the number of prey items delivered per load ($F_{2, 78} = 0.46$, $P = 0.63$).

Based on these results, I used the number of loads provided per day to analyse differences in provisioning rates between males and females.

The provisioning rate of razorbills differed significantly between the sexes (females: 2.02 ± 0.11 loads day $^{-1}$, $N = 19$; males: 1.42 ± 0.09 loads day $^{-1}$, $N = 19$; two-

way ANOVA: $F_{1, 108} = 18.94$, $P < 0.001$), but not with chick age (one week: 1.67 ± 0.12 loads day $^{-1}$; two week: 1.83 ± 0.12 loads day $^{-1}$; three week: 1.65 ± 0.16 loads day $^{-1}$; $F_{2, 108} = 0.72$, $P = 0.491$). However, the interaction term sex* chick age was significant ($F_{2, 108} = 4.48$, $P < 0.02$). Further analysis of the main factors showed that sexes did not differ on the feeding rates when chicks were less than one week old (ANOVA: $F_{1, 36} = 0.49$, $P = 0.49$; Figure 6.5), but the feeding rates of females were significantly higher than those of males when chicks were two (ANOVA: $F_{1, 36} = 4.50$, $P = 0.04$) and three weeks old (ANOVA: $F_{1, 36} = 20.47$, $P < 0.001$; Figure 6.5). Provisioning rates of males differed among chick-age groups (ANOVA: $F_{2, 54} = 4.04$, $P = 0.02$), with males feeding one-week old chicks significantly more frequently week than older chicks (Tukey HSD: $P = 0.04$). Provisioning rates of females did not vary with chick age (ANOVA: $F_{2, 54} = 1.65$, $P = 0.20$; Figure 6.5). The combined chick provisioning per pair did not vary with chick age (ANOVA: $F_{2, 54} = 1.02$, $P = 0.37$; Figure 6.5).

The length of prey items was calculated as a proportion of the gape length of males and females. The gape length was significantly larger in males (5.42 ± 0.04 cm, $N = 28$) than in females (5.25 ± 0.05 cm, $N = 34$; Student t-test: $t_{60} = -2.59$, $P = 0.01$). I inferred that females delivered prey items that varied between 2.63 and 15.75 cm long, and males delivered prey items between 4.07 and 16.26 cm long. I used the mean length of multiple-prey loads for the comparison between sexes because no significant differences were found in the number of prey items per load (see above). The mean length of prey items did not differ between females (9.82 ± 0.17 cm, $N = 14$) and males (10.19 ± 0.21 cm, $N = 14$; two-way ANOVA: $F_{1, 78} = 1.69$, $P = 0.20$) or among chick-age

groups (one week: 9.90 ± 0.29 cm, $N = 28$; two week: 9.82 ± 0.17 cm, $N = 28$; three week: 10.06 ± 0.24 cm, $N = 28$; $F_{2, 78} = 0.13$, $P = 0.88$). There was no interaction of the main factors on the mean length of prey items ($F_{2, 78} = 0.078$, $P = 0.93$).

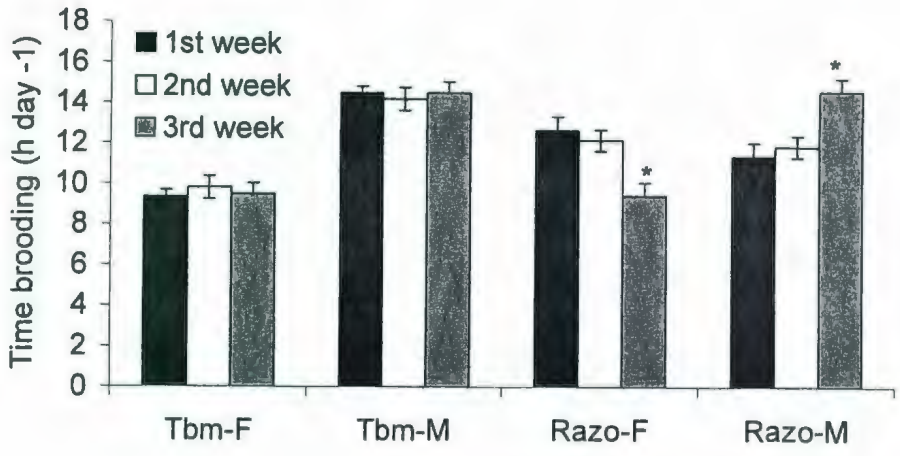

Figure 6.4 Sex differences on the brooding duration of thick-billed murres ($N = 13$ pairs) and razorbills ($N = 21$ pairs) according to chick age categories. Data are shown as means ± SE. Statistical differences within sexes were only for razorbills (*Turkey HSD: $P < 0.01$).

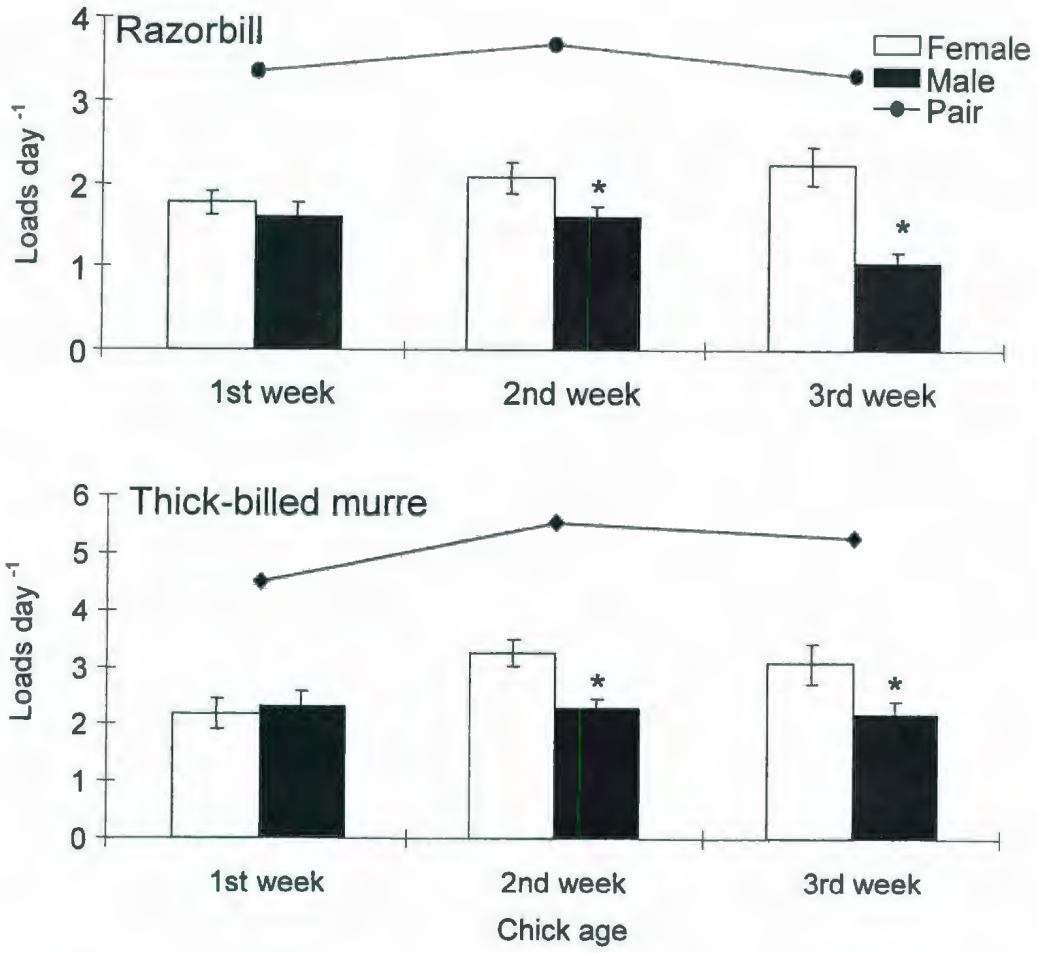

Figure 6.5 Provisioning rates (Means ± SE) of male and female razorbills ($N = 19$ pairs) and thick-billed murres ($N = 13$) according to chick age categories at Gannet Islands, Labrador. Statistical differences between sexes in each category are shown (* ANOVAs, $P < 0.05$). No significant differences of the total chick provisioning were found among chick age categories in both species (ANOVAs, NS).

6.4.4 Foraging trip frequency and duration

6.4.4.1 *Thick-billed murres*

During the chick-rearing period, murres performed a mean of 3.72 ± 0.12 foraging trips per day (range 1 - 8) that lasted an average of 1.90 ± 0.11 h (range 0.17 - 12 h). Foraging trips with food delivery to the chick occurred after absences from the breeding site of 10 or more minutes. Overall, females performed significantly more foraging trips per day than males did (two-way ANOVA: $F_{1, 72} = 7.21$, $P < 0.01$, Table 6.1). The number of foraging trips did not depend on chick age (one week: 3.40 ± 0.20 trips day $^{-1}$, $N = 26$, two week: 3.90 ± 0.20 trips day $^{-1}$, $N = 26$, three week: 3.85 ± 0.20 trips day $^{-1}$, $N = 26$; $F_{2, 72} = 1.90$, $P = 0.16$) and no interactive effect of the main factors was detected ($F_{2, 72} = 0.81$, $P = 0.45$). Similar results were found when individual differences were controlled using a paired comparison of the foraging trip frequency per breeding site between sexes (paired *t*-test: $t_{12} = 2.89$, $P = 0.01$).

The duration of foraging trips of males was significantly longer than that of females (log-transformed data, two-way ANOVA: $F_{1, 72} = 85.39$, $P < 0.001$, Table 6.1). Foraging trip duration did not vary with chick age ($F_{2, 72} = 2.321$, $P = 0.11$) and the interaction term sex*chick-age group was not significant ($F_{1, 72} = 0.94$, $P = 0.40$). Similar results were found between sexes when their foraging trip durations were matched per breeding site (paired *t*- test: $t_{12} = -6.39$, $P < 0.001$). The mean duration of foraging trips that ended in chick provisioning was significantly longer for males than for

females (log-transformed data: ANOVA: $F_{1, 24}$: 47.95, $P < 0.001$, Table 6.1). Foraging trips without chick provisioning did not differ significantly between sexes (female: 1.28 ± 0.10 h; male: 1.42 ± 0.21 h; ANOVA: $F_{1, 24}$: = 0.39, $P = 0.54$).

6.4.4.2 *Razorbills*

During brooding, a mean of 3.21 ± 0.09 (range 1-14) foraging trips was performed per day, lasting on average 2.18 ± 0.09 h (range 0.17 - 11.83 h). Foraging trips with food delivery occurred after absences from the breeding site of 10 or more minutes. The total number of foraging trips per day did not differ between sexes (two-way ANOVA: $F_{1, 120} = 1.76$, $P = 0.19$, Table 6.1), nor with chick age (one week: 3.08 ± 0.14 trips day $^{-1}$; two week: 3.15 ± 0.17 trips day $^{-1}$ three week: 3.38 ± 0.16 trips day $^{-1}$; $N = 42$; $F_{2, 120} = 1.04$, $P = 0.35$). There was no interactive effect of the main factors on the number of foraging trips ($F_{2, 120} = 1.88$, $P = 0.16$). Similar results were found between sexes when their mean number of trips was matched per breeding site (paired t-test: $t_{20} = -1.04$, $P = 0.31$). However, females had significantly more foraging trips with food delivery (see chick provisioning) than males (Table 6.1).

Foraging trip duration did not differ between the sexes (log-transformed data: two-way ANOVA: $F_{1,120} = 0.400$, $P = 0.53$, Table 6.1) or with chick age (one week: 2.03 ± 0.24 h; two week: 2.06 ± 0.22 h; three week: 1.85 ± 0.27 h; $F_{2, 120} = 0.71$, $P = 0.49$). No interactive effect of the main factors on trip duration was detected ($F_{2, 120} = 0.63$, $P =$

0.54). Similar results between sexes were found after matching the mean duration of trips per breeding site (paired *t*-test: $t_{20} = -1.38$, $P = 0.18$). In contrast, the duration of foraging trips with food delivery was significantly longer for males than for females (ANOVA: $F_{1, 42} = 10.15$, $P < 0.01$, Table 6.1). The mean duration of trips without food delivery did not differ between sexes (female: 1.42 ± 0.18 h; male: 1.10 ± 0.15 h, ANOVA: $F_{1, 42} = 0.02$, $P = 0.88$).

Table 6.1 Foraging trips of female and male Thick-billed murres (13 pairs) and Razorbills (21 pairs) at Gannet Islands, Labrador.

	Thick-billed murre		Razorbill	
	Female	Male	Female	Male
Number of trips per day	4.02 ± 0.22*	3.40 ± 0.23	3.09 ± 0.11	3.32 ± 0.13
Number of trips with meal delivery	2.84 ± 0.21*	2.26 ± 0.11	2.02 ± 0.12*	1.42 ± 0.13
Trip duration[1] (h)	1.19 ± 0.23	2.40 ± 0.21*	1.93 ± 0.20	2.03 ± 0.15
Trip duration with meal delivery[1] (h)	1.23 ± 0.41	3.04 ± 0.33*	2.50 ± 0.42	3.30 ± 0.21*

Means are given ± SE. Significant differences between sexes are shown (*ANOVAs, $P < 0.01$).

[1]Data were log-transformed before the statistical analysis.

6.5 DISCUSSION

I studied two sympatric Alcini species, thick-billed murres and razorbills that have biparental care at the breeding site followed by exclusively paternal care at sea (Gaston & Jones 1998). My objective was to determine inter and intra-specific patterns of parental roles between sexes to be able to understand why the male accompanies the chick to sea. Although a widespread tendency for paternal care late in chick rearing exists in Charadriiform birds (Gratto-Trevor 1991; Piersma 1996a; Piersma 1996b; Payne & Pierce 2002), it is relatively rare among the alcids (4 of 23 extant species). Thus, my approach was to identify characteristics of two alcid species that could favour such a pattern.

6.5.1 Intra-specific patterns

I found different patterns in the time devoted to incubation by males and females between species. Both parents spent a similar amount of time incubating eggs in thick-billed murres, but female razorbills had longer incubating bouts than males. Common murres at the Gannet Islands behave similarly to thick-billed murres, that is females and males do not differ in the duration of incubation bouts (Verspoor *et al.*1987). Likewise, female razorbills in the Gulf of the St. Lawrence, Quebec (Bédard 1969) behave similarly to

those at the Gannet Islands. Differences in levels of male effort during mate guarding prior to egg-laying may explain the different incubation patterns between species. Razorbills have more occurrences of extra-pair copulations than murres (Wagner 1992; Hipfner & Chapdelaine 2002) and they need to commute between two locations, mating arenas and breeding sites, for mate guarding. Thus, male razorbills may start the incubation period in poorer condition than male murres and, for this reason, may be more selective in their parental duties and effort allocation. For example, if males are better than females in defending the nest, it would be of benefit to both parents for the male to spend more time and effort defending the nest than incubating (see intra-specific patterns below).

Thick-billed murres showed a consistent pattern in the timing of breeding site attendance during the incubation and brooding period. Most males incubated eggs or brooded chicks during early morning, late afternoon and, usually, over night. In contrast, females incubated eggs or brooded chick mostly during the middle of the day. Likewise, females had a bimodal period of chick feeding; 41% and 51% of their feedings occurred early in the morning and late in the afternoon respectively. Males had a single and long period of chick feeding during the day; however about half of their feeding occurred between 13:00-16:00 h. These results support a previous chick-rearing study of murres, which used radio-transmitters and temperature loggers at Gannet Is. That study found that males foraged during the day and females foraged mostly before sunset and after sunrise (Jones *et al.* 2002). Conversely, but consistent with these results, another study reported that female common murres at Gannet Is.; incubated eggs during the day whereas males

did so during the night (Verspoor 1987). In contrast, I found that razorbills do not show sex differences in the timing of breeding site attendance and chick feeding. Males and females were found incubating or brooding at similar times of the day, as was found in a previous study of razorbills at the Isle of May (56 °N; Wanless & Harris 1986). Likewise, both sexes fed their chicks all through the day; and showed two small peaks of prey delivery early in the morning and early in the afternoon. During reproduction, thick-billed murres and razorbills are central place foragers, so traveling and searching effort can affect chick-provisioning (Orians & Person 1979) and therefore reproductive performance (Clode 1993). Because murres are single loaders and deep-pursuit divers (Gaston & Jones 1998), the division of foraging time between sexes initiated during the incubation period may help to maximize their foraging effort during chick-rearing. In fact, several studies have shown the ability of murres to memorize and locate "hot spots" of food during reproduction (Cairns & Schneider 1990; Davoren *et al.* 2003), and their strong fidelity to foraging areas at spatial scales of 1-20 km (Mehlum *et al.* 2001). On the other hand, razorbills are multiple prey loaders and shallow divers (see review by Hipfner & Chapdelaine 2002), suggesting that they might use different tactics than murres to reduce their foraging effort at sea. According to central place foraging theory, multiple prey loaders are expected to forage closer to the colony to reduce traveling time; if this is the case for razorbills require further investigation. In addition, the time spent searching within food patches is likely to be less for razorbills than for murres, as razorbills performed shorter dives to capture their prey higher in the water column or in shallow water (review by Hipfner & Chapedelaine 2002). Thus, razorbill's searching effort may

not be as constrained as that of murres, and a strict division of foraging times between males and females may not be mandatory.

6.5.2 Inter-specific patterns

I hypothesized that sex-specific differences of murres and razorbills in energy expenditure at the time of departure may explain why males accompany chicks to sea. I expected parental care at the breeding site of both species to be mostly female-biased due to the male's initial expenditure of effort on mate guarding prior to egg-laying. I further expected that this would lead to males being in better condition than females at the time of departure to finish raising the chick at sea.

Incubating and brooding both seem to be energetically less expensive than chick provisioning in thick-billed murres (Gaston 1985) and probably in razorbills. Foraging at sea for chick provisioning is the most time- and energy-consuming activity for seabirds (e.g. Chappell *et al.* 1993), especially for flapping-flight and pursuit-diving species (Birt-Friesen *et al.* 1989; Obst & Nagy 1992; Bech *et a*l. 2002; Jodice *et al.* 2003), such as the large auks (Gaston & Jones 1998). In fact, thick-billed murres rearing chicks reduced their feeding rates and body mass, and have longer foraging trips when handicapped with data loggers (Paredes *et al.* 2005). As I predicted, I found that in both auk species males spent more time with chicks and provided fewer meals per day than females, although these results depended somewhat on chick age. Razorbill males spent more time with

chicks greater than two weeks old, while murre's allocation of care did not differ among chick age groups (1-3 weeks). Nevertheless, males of both auk species spent more nights with chicks during the brooding period than females. In both species, males reduced their provisioning rates when chicks were more than a week old. I did not find differences in the prey sizes delivered by males and females in either species. Higher female contribution toward chick provisioning has been reported in common murres at Isle of May (Wanless & Harris 1986) and at Witless bay, NL (Wilhelm 2004). However, no extra-male allocation toward brooding has been reported in common murres (Wanless & Harris 1986; Verspoor 1987; Wilhelm 2004). In razorbills, approximately equal parental contribution to night nest attendance and chick feeding has been reported at Skomer Is. (Wagner 1992). These differing results may be explained by methodological differences; slight sex differences in parental behaviour might be less likely to detect when using sub-sample observations (other studies) instead of continuous daylight sampling (this study). Different foraging strategies within and between species may also affect parental behaviour in other localities (see intra-specific patterns). In dovekies, differences in nest attendance and chick provisioning only occur during the late chick-rearing period; females depart the colony and males provide all the care until chick departure (Harding *et al.* 2004). Assuming breeding site visitation was a reliable method to assess feeding rates in crevice nesters that feed regurgitated food (see Granadeiro *et al.* 1999), these different results may be explained by breeding biology. Because dovekie chicks depart with the male when almost full grown (67-82% of adult body mass), the time and effort males need to allocate at sea is likely to be less than for murres and razorbills (chicks 15-30% of

adult body mass). In addition, flying in smaller dovekies may involve less effort than in larger auks. Thus, increased provisioning by the male at the end of the chick-rearing period may not be an energy constraint during reproduction.

By analyzing only foraging trips with meal delivery, I found that males of both species performed longer trips while females performed shorter, but more frequent trips, than males. These results suggest different foraging strategies between males and females, such as traveling to different foraging areas and/or diving at different levels of the water column when searching for food. In thick-billed murres, sexes do not differ in their dive depth or duration (Jones *et al.* 2002; Chapter 2) and other dive parameters (Chapter 2) when capturing prey for chick provisioning. However, the return trips of males after the last dive and before chick feeding were longer in duration than those of females (Chapter 3). Murres are likely to fly directly back to the colony from their foraging areas because they deliver a single fresh fish to their chicks (Benvenutti *et al.* 1998). Thus, if males travel farther to forage their flying costs for chick provisioning are likely to be higher than those of females. No data are available for razorbill diving behaviour between sexes so I was unable to determine whether the longer foraging trip durations of male razorbills were due to different foraging areas, diving effort or both. Nevertheless, the longer foraging trips of males are probably as energetically costly as the more frequent trips of females with meal delivery. Thus, the overall effort for chick provisioning is not likely female-biased as I predicted.

In relation to the role of breeding site defence, I found another interesting pattern in the time and activities of male and female parents at the breeding site when their mates

were incubating or brooding. According to Birkhead (1978; 1985), the off-duty parent generally defends the breeding site, while the on-duty parent avoids such aggressive interactions. I found that in both species males spent more time interacting aggressively with neighbours or intruders and preening their mates than females during incubation and brooding. These results are more suggestive of a male-biased role toward the defence of the breeding site, guarding of the mate and protection of the offspring. The extra time males spent at the breeding site may be important to reinforce long-term bonds and to ensure breeding site ownership, as males will leave earlier than females. Thus, male allocation of risk and effort toward the defence of the breeding site, egg or chick, and mate seems to be higher than that of females before chick and male departure to sea, which also contradict my prediction of equivalent parental care between sexes before chick and male departure.

In summary, I found males and females had different parental roles, but the level of parental effort at the breeding site does not seem to be female-biased as I hypothesized. In fact, the opposite seems to be true, males spent more time brooding and defending the nest than females, while the total allocation in chick feeding seems to be sex balanced. After the initial effort of males and females in mate guarding and egg production, respectively, they seem to be able to recover their energy expenditure while engaged in their parental roles during incubation. During this time, foraging is less costly and entirely focused on self-feeding. Flying and diving effort appears to be lower than during brooding because commuting between feeding areas and breeding sites is less

frequent (this study), and they feed on prey located in shallower water (Benvenuti *et al.* 2002). Later on, males and females might be in reasonable shape to start taking care of the chick at the breeding site. Although I was unable to measure energy expenditure, my indirect measurements of parental effort (time and frequency of events) suggest an equal if not a male-biased parental effort at the breeding site. Thus, differences between males and females in energy expenditure do not explain the male's parental role at sea, as their condition is likely to be equal or lower than that of females at the time of departure. Instead, I believe that the most likely explanation for the patterns of parental roles found between sexes was the result of a chain of events favouring male involvement in chick brooding and care at sea (Figure 6.6).

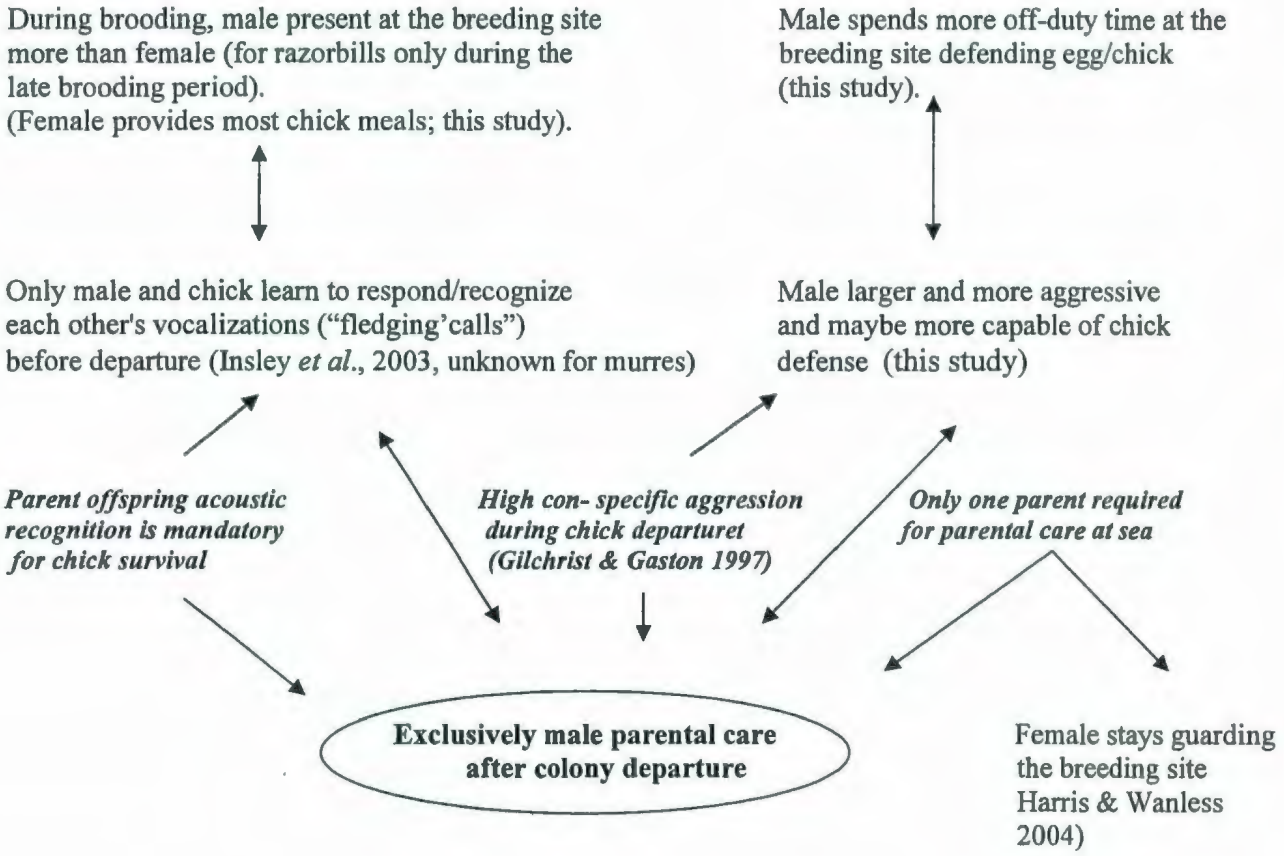

Figure 6.6 Patterns of parental roles of female and male thick-billed murre and razorbill at Gannet Islands, and proposed explanation of male only care at sea.

A longer time spent brooding the chick by males may also benefit the development of parent-offspring acoustic recognition, which is crucial for chick survival at breeding site departure. Lefreve *et al.* (1998) reported that in thick-billed murres chick and parents were able to recognize each other's calls when the chick was three days old. They also reported that parents recognize their chicks' calls at fledging age, when chicks produced a unique "fledging" call. Unfortunately, the sex of the birds in this study was not known. However the sample might have been male-biased, as suggested by the time of the day the recordings were made. I observed one incident in which a female murre did not respond to its chick's "fledging" calls (c. 1 m apart) when it was left alone by the male during colony departure. The calling chick was pecked several times by other adults, without reaction from the female, which stayed at the breeding site, and eventually departed alone.

Whether or not there is a sex-biased parent-offspring vocal recognition in thick-billed murres requires further investigation. In razorbills, the onset of vocal recognition occurs during the last week before departure (Ingold 1975; Insley *et al.* 2003), and it is only the male that appears to recognize its chick's calls, or at least responds to them (Insley *et al.* 2003). Other studies of alcids with different modes of development (Sealy 1973) suggest that onset of recognition occurs when spatial cues are not sufficient to prevent misidentification (Harris 1983; Jones *et al.* 1987). Murre breeding sites are less discrete and denser than those of razorbills, so the risk of chicks intermingling is higher. Thus, in comparison to razorbills parent-offspring mutual recognition by male and female

murres is needed at an early stage. Later on, a longer investment of time at the breeding site by males of both species may be required to learn their chicks "fledging's" calls and ensure parent-offspring recognition at departure. Like murres and razorbills, dovekies males also spent more time at the nest site than females during late chick-rearing period (Harding *et al.* 2004), which suggest male-biased time brooding may also function as a way to ensure parent-offspring vocal recognition at departure.

One of the main causes of murre chick mortality at departure is the aggressive interaction from neighbours at the colony and co-specifics at sea (Gilchrist & Gaston 1997). My findings of a male-biased role towards the defence of egg and chick at the breeding site suggest sex differences in aggressive behaviour (see also Fraser *et al.* 2002). A larger and more aggressive sex may be more successful in protecting the chick during and after departure. All members of the Alcini tribe are slightly dimorphic species, with males being larger in mass and in most morphological dimensions (Gaston & Hipfner 2000; Wagner 1999; Gaston & Jones 1998). In addition at Gannet Islands, males of both thick-billed murres and razorbills seem to be more aggressive and protective of their chicks than females (Chapter 4). Ainley *et al.*, (2002) suggested that in common murres, males depart with the chick because of their slightly larger size and apparently more aggressive behaviour; however, few data have been reported so far. Altogether these results suggest a male-biased capability of defending the offspring at nest departure, and partly could explain why the male accompanies the chick at sea.

Another explanation for the partitioning of roles between sexes, although not mutually exclusive, is that the male goes to sea as a default of the female's choice of staying behind. One pair member seems to be required to stay at the colony to maintain the breeding site for the following season (Harris *et al.* 1996). Maintenance of the breeding site is crucial because if lost, it is likely that individuals will not breed the following year (Harris *et al.* 1996). In all my study pairs, males left the colony with the chick and females stayed at the breeding site. It has been suggested females stayed at the breeding site for mating with other males to ensure future reproductions in case of mate loss or poor quality partner (Gaston & Jones, 1998). However, although females can copulate and form temporary bonds with other males these do not persist to the next season, even when the original males did not return (Harris & Wanless, 2003). Thus, there is no support for female looking for replacement mates in case of widowing, but toward the female role of guarding the breeding site after male departure.

Both, escorting the chick at sea and guarding the breeding site after chick departure may require an aggressive sex. Nevertheless, a successful chick departure and fledging at sea is crucial for the fitness of both parents. Hence, a higher level of aggressiveness of the parent that escorts the chick to sea may have been selected for to ensure offspring survival. As a result, male parental role towards egg and chick defence (male-biased capability) and brooding (parent-offspring vocal recognition) might have developed at the breeding site at the same time or independently to ensure male-only care at sea.

6.6 ACKNOWLEDGMENTS

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CHAPTER 7: SUMMARY AND FINAL REMARKS

This study aimed to elucidate parental roles and foraging strategies of males and females of two sympatric closely related large auk species, thick-billed murres and razorbills at Gannet Islands, Labrador. They raise a single offspring, which departs with the male parent after 15–20 days of biparental care at the breeding site and completes its development at sea over the following 3–4 weeks.

I hypothesized that sex-specific differences in effort allocation at the time of departure could explain why males accompany chicks to sea. I expected parental care at the breeding site of both species to be mostly female-biased due to the male's initial expenditure of effort on mate guarding prior to egg-laying. I further expected that this would lead to males being in better condition than females at the time of departure to finish raising the chick at sea. Because these species are wing-propelled diving species, I first analyzed their diving behaviour and diet to determine possible relationships of foraging strategies and parental roles. I specifically quantified sex differences in: 1) effect of external data loggers in parental and foraging behaviour, 2) diving behaviour in relation to prey species captured, 3) diving behaviour for self-feeding and chick provisioning, 4) aggressive behaviour of attending birds, and 5) parental roles at the breeding site.

My conclusions, briefly…

1. Individual thick-billed murres' body condition and behaviour (brooding, feeding, foraging duration) was negatively affected by carrying time-depth recorders (TDRs) when compared to non-instrumented birds (control). These results were likely to be due to a reduction of birds' diving and/or flying performance, so I was aware that my measurements were likely under or overestimates. Both sexes were similarly affected except for body mass and foraging trip duration; males lost mass at a higher rate and had longer trips than females. Males' longer return trips after diving for provisioning suggest males had farther feeding areas than females. These results support the idea that the effect of data-loggers in murres' flying performance was due to their high wing loading. On the other hand, sexes of murres and razorbills did not differ in the number of dives per bout and per day and both were able to dive at similar maximum depths, which suggested no differential TDR effect of the sexes underwater. Because males and female thick-billed murres and razorbills are almost identical in mass and morphometrics, and were treated identically in my procedures, I cautiously assumed that sex differences in foraging behaviour would occur as a result of naturally different strategies and not due to the effect of attached devices.

Partners of TDR-equipped birds compensated for the reduced parental effort in brooding and chick provisioning of their mates, with no differential responses between sexes. As a result of this behaviour, overall breeding success of TDR-equipped pairs (only one bird with TDR) did not differ from that of control pairs. TDR-equipped birds also had a significantly lower rate of return to breed than their non-equipped partners or control birds, and those that did return the following season were more likely to change mates

(32%) compared with controls (0%). Although, compensatory behaviour observed in thick-billed murres seem to be a necessary response for breeding success in this single brooded species, it might also affect the stability of pair bonds of some individuals

2. Differences in diving behaviour and secondary prey preference were found in female and male thick-billed murres and razorbills. Differences in diving behaviour were mainly in their dive profiles, which are likely related to specific capturing strategies and prey species. In thick-billed-murres, differences in diving behaviour were strongly related to the time they foraged; males dived deeper than females and mostly between mid-day and early afternoon, while females mostly dived around dawn and dusk. Because depth directly affects other dive parameters, male murres also had longer bottom time, ascent and descent rates, duration, and post-dive interval. These differences disappeared when depth was controlled for, except for post-dive interval (PDI). Longer female's PDI may be explained by their slightly smaller size (c. 5 % of body mass) and therefore lower gas-storage capacity than males. In razorbills, there was not a clear division in timing between the sexes nor were there differences in their main dive parameters. Nevertheless, female razorbills dived somewhat more frequently in shallower waters (< 10 m) and at twilight periods than males as shown by female murres. These results explained the shorter dive bouts found in females of both species despite the similar number of dives per day and bout between the sexes. This temporal segregation in depths between sexes was reflected in their dive shapes and prey species. U-shaped dives were deeper and male-biased, and W-shaped dives were shallower and female-biased in both species. V-

shaped dive was mostly performed by razorbills. Although both sexes delivered mostly a primary prey species (murres: daubed shanny; razorbills: sand lance); both male species delivered more capelin than females. Analysis of foraging time, dive-shapes and preys delivered suggest a relationship between dive profile and prey species: a) W-shaped dived and crustaceans, mainly captured by females at twilight periods, b) U- and square shaped dives and mid-deep water species such as capelin and daubed-shanny, and c) V-shaped dives and shallow water species such as sandlance.. Altogether, my results suggest a temporal segregation of water depths and food resources between the sexes in two sympatric and closely related species during reproduction. Sex differences in nest attendance, driven by differences in parental roles, seem to explain these findings.

3. Further analysis of the foraging behaviour of male and female thick-billed murres showed differences in diving behaviour for self-feeding and distance to foraging areas as well. Females' dive bouts for self-feeding were shallower than males and occur mainly around dawn. Males' dives for self-feeding were deeper than those of females and occur during and between trips for chick provisioning. In contrast, chick- provisioning diving was deeper than self-feeding irrespective of the sex or the time of day. This suggests equal parental effort allocation of the sexes underwater. Assuming murres return directly to the colony after the last dive at sea, shorter female's return trips suggest they feed in closer areas to the colony than males. Higher self-feeding rates and closer feeding locations may partially explain female's higher delivery rates at the breeding site.

4. Attending male and female thick-billed murre and razorbills differed in the level of aggressive behaviour at the Gannet Islands, Labrador. Frequency but not intensity of aggressive behaviour against con-specific intruders was higher in males in both species. Both frequency and intensity of aggressive responses to a predator model was higher in male than female razorbills. The larger bill dimensions found in both male species may confer a better ability for defending or protecting the egg or offspring. The defence of the chick at departure, and at sea is crucial for its survival and therefore parents' fitness. Thus, a more aggressive and better equipped sex may be better in protecting the chick at departure.

5. Female and male thick-billed murre and razorbill differ in their parental roles at the breeding site. Females provided more meals to the chicks and males spent longer time periods brooding than females. These results were chick-age dependant in each species. Murres showed a consistent pattern of breeding site attendance between sexes throughout the incubation and brooding period; females brooding during mid-day and early afternoon and males during twilight and night periods. Razorbills' breeding site attendance schedules were much more variable and did not differed between the sexes. Despite these differences in timing of breeding site attendance between species, males of both species spent twice as much time as females engaged in the defence of the egg or

chick at the breeding site, consistent with my previous observations of male-biased capability of protecting the chick at departure.

I found males and females had different parental roles, but the level of parental effort at the breeding site did not seem to be female-biased as I had originally hypothesized. Although I was unable to measure energy expenditure, my indirect measurements of parental effort (time and frequency of events) suggest an equal if not a male-biased parental effort at the breeding site. Thus, differences between males and females in energy expenditure did not explain the male's parental role at sea, as their condition was likely to be equal or lower than that of females at the time of departure. Instead, I believe that the most likely explanation for the patterns of parental roles found between sexes was the result of a chain of events favouring male involvement in chick brooding and care at sea. A successful chick departure and fledging at sea is crucial for the fitness of both parents. Hence, a higher level of aggressiveness of the parent that escorts the chick to sea may have been selected for to ensure offspring survival. As a result, male parental role towards egg and chick defence (male-biased capability) and brooding (parent-offspring vocal recognition) might have developed at the breeding site at the same time.

Final remarks

The evolution of predominant male care among monogamous birds is not well understood. One possible explanation is that high costs of egg production constrain females' ability to incubate or to care take of the offspring; however increasing evidence suggest they can recover by re-arranging activities of feeding more (Amat *et al.* 2000; Wilhem 2003; Williams 2005). Re-mating opportunities seem to explain the desertion of females in populations with male-biased ratios (e.g. Székely 1996; Székely *et al.* 2006). Another possible explanation is that there are relatively few species where biparental care is share exactly equally between the sexes (Clutton-Brock 1991). For instance, in many monogamous species males are more involved in territory defense than females, while females spend more time caring for the young (e.g. Breitwish 1988). The fact that male major involvement in nest defense persists during the chick-rearing period (Hogstad 2005; Winkler 1992; Lombardo 1991; Regelmann & Curio 1986; Sproat & Ritchison 1993, Kis et al. 2000; Pierotti 1981; Southern 1981; Creelman & Storey 1980) suggests that defensive behaviour is driven by the offspring needs. My study supports this and further indicates greater ability of males of defending the offspring because of their more aggressive and larger bill size (weapondry). The persistence of these morphological and behavioural traits (i.e. bill size, aggressive behaviour) in truly monogamous males suggests they were selected for parental rather than for a sexual function. Differential abilities in parental duties (e.g. offspring defense) may explain how males and females divide parental roles.

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